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A Critical Review of Laboratory Multispecies Tests

Oak Ridge National Lab., TN

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A Critical Review of Laboratory Multispecies Tests

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This document provides a review and evaluation of laboratory methods for measuring the effects of chemicals on aquatic and terrestrial population interaction and ecosystem properties. The use of mathematical models in ecotoxicological assessment is also addressed. More than 450 references are cited and a bibliography of 700 references is included.

Laboratory tests are evaluated for their potential for standardization for use in the ecological hazard and risk assessment processes under the Toxic Substances Control Act. The criteria used for these evaluations include whether or not the tests are: rapid, reproducible, relatively inexpensive, unequivocal, sensitive, socially and economically relevant, predictive, generalizable, and well-developed.

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METHODS FOR ECOLOGICAL TOXICOLOGY
A CRITICAL REVIEW OF LABORATORY MULTISPECIES TESTS

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FOREWORD

The scientific disciplines of ecology and environmental toxicology have not been communicating adequately with each other, to the detriment of both. Ecologists are often falling short when it comes to applying the theory and findings of their relatively young science in useful practice to meet society's needs for assessment of the environmental impacts of toxic pollutants. Environmental toxicologists are increasingly having difficulty in trying to convince society's decision makers what the results of their test methodologies in simple systems really mean in a complex, highly interactive ecological world.

This report takes a step toward marrying some of the concepts of these two scientific disciplines. At the request of the Environmental Protection Agency's Office of Toxic Substances, the Environmental Sciences Division of Oak Ridge National Laboratory has reviewed and evaluated potential techniques for studying ecological effects of toxic chemicals in systems that transcend the practicable but oversimplified conditions of most currently used toxicological test systems.

EPA intends to use this study, and companion efforts, to help guide our future attempts to bring about better synergy between ecology and environmental toxicology in our implementation of the Toxic Substances Control Act.

James J. Reisa

James J. Reisa, Ph.D.
Associate Deputy Assistant Administrator
for Toxic Substances
U.S. Environmental Protection Agency

PREFACE

This report was prepared by the Environmental Sciences Division, Oak Ridge National Laboratory, under an Interagency Agreement between the Department of Energy and the Environmental Protection Agency.

The study was undertaken because of the need to examine the potential for development and standardization of tests for effects of chemical substances on selected ecological parameters that are indicative of interspecific interactions, community dynamics, and ecosystem functions.

Aquatic and terrestrial laboratory methods for measuring the effects of chemicals on population interactions and ecosystem properties are discussed and evaluated for use in ecological hazard and risk assessment processes. The report is not intended to provide detailed descriptions of all suitable tests. Instead, it is intended to provide a critical review of useful or potentially useful ecological tests (i.e., those most amenable for laboratory test development) for consideration by various technical and administrative personnel responsible for implementing the Toxic Substances Control Act.

Although an extensive review of mathematical models was not included in the scope of this study, a general discussion of the roles of broad categories of models in ecotoxicology is provided. The document is a useful resource for ecologists, environmental toxicologists, and scientists interested in the application of mathematical models to environmental hazard and risk assessments.

ABSTRACT

This report critically evaluates selected laboratory methods for measuring ecological effects and recommends tests considered most suitable for research and development for use in predicting the effects of chemical substances on interspecific interactions and ecosystem properties. The role of mathematical models in chemical hazard assessment is also discussed. About 450 references are cited. A bibliography of more than 700 references is provided.

The Office of Toxic Substances, U.S. Environmental Protection Agency (EPA) is responsible for implementing the Toxic Substances Control Act (TSCA). TSCA, promulgated in 1976, is comprehensive legislation designed to broadly protect human health and the environment from unreasonable risks resulting from the manufacture, processing, distribution, use, and disposal of a chemical substance.

Under TSCA, EPA is responsible for identifying and prescribing test standards to be used in developing the data necessary to predict the risks associated with chemical releases into the environment. To aid EPA in this endeavor, laboratory methods for measuring the effects of chemical substances on aquatic and terrestrial interspecific interactions and ecosystem processes were reviewed and evaluated for their potential for standardization for use in environmental hazard and risk assessment processes. The criteria used for these evaluations include whether or not the tests are: rapid, reproducible, relatively inexpensive, unequivocal, sensitive, socially relevant, predictive, generalizable, and well-developed.

This report was submitted in partial fulfillment of Interagency Agreement No. EPA 78-D-X0387 between the Department of Energy and the U.S. Environmental Protection Agency.

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SECTION 1

INTRODUCTION

1.1 Purpose

The voluminous production of chemicals since World War II has significantly increased the potential for exposing the general public to toxic substances. More than 44,000 chemicals have been listed in the Toxic Substances Control Act Chemical Substances Inventory: Initial Inventory, published in May 1979 by the Environmental Protection Agency (EPA 1979a), and new chemicals are added to the market at the rate of several hundred per year. Sources of exposure range from foods and other consumer products to waste disposal sites and polluted air and water. Increasing concern about the effects of such exposure led to the development of deliberate and comprehensive legislation, the Toxic Substances Control Act (TSCA), which was promulagated in 1976. The Office of Toxic Substances, EPA, is responsible for implementing TSCA.

Other laws have been enacted that give the federal government authority to regulate chemical substances. Some agencies responsible for such regulation include the Food and Drug Administration, Consumer Products Safety Commission, Occupational Safety and Health Administration, U.S. Department of Agriculture, and the U.S. Department of Transportation. For the first time, TSCA subjects the entire chemical industry in the United States to federal regulation that broadly protects human health and the environment from unreasonable risks resulting from the manufacture, processing, distribution, use, and disposal of a chemical substance. Requirements under this law include testing of chemicals identified as possible risks and controlling chemicals proven to present a risk. The most significant aspect of TSCA is that regulatory action can be taken before widespread exposure and possible serious damage have occurred. Therefore, justification for such action must be based on the predicted effects of specific chemicals on human health and the environment.

Under TSCA, EPA is responsible for identifying and prescribing test standards to be used in developing data necessary to predict the human health and ecological risks associated with releases of chemical substances into the environment. EPA has recognized a set of standard toxicity testing procedures for assessing the environmental hazards of chemicals (U.S. EPA 1979). These procedures are simple, rapid, inexpensive, and easily applied to large numbers of chemicals in laboratories throughout the country. Each test measures a direct toxic response (usually death) of an organism or group of organisms of a single species. The primary objective of such tests is to screen or compare chemicals and to rank them according to their relative toxicity. Chemicals ranking low in toxicity are presumed to pose no ecological hazard; chemicals ranking high in toxicity are subjected to further testing. The success of a hazard assessment program depends (1) on the ability of the screening tests to correctly identify potentially hazardous chemicals and (2) on the availability of advanced test methods to confirm and refine the results of screening tests and to define the suspected environmental hazards more precisely.

There is substantial evidence that some chemicals can produce effects on organisms that do not result in death in single-species toxicity tests, but that nevertheless impair the ability of the organism to survive under actual ecological conditions. For example, polychlorinated biphenyls (PCBs) in concentrations well below the lethal levels alter the behavior of grass shrimp to such an extent that the shrimp become more vulnerable to predation by fish; this effect is not readily detectable unless the fish are present (Tagatz 1976; Farr 1977). The same compounds impair the nutrient uptake capability of some marine diatoms, an effect that becomes apparent only when the diatoms are competing with other algal species for nutrients (Fisher et al. 1974). Effects such as these, which depend on interactions between populations for their manifestation, can be just as significant in a realistic ecological context as the more easily measured direct toxic effects.

A suitable scheme for identifying and evaluating hazards to environmental systems should include tests for predicting effects on events and processes occurring above the single-species level. Therefore, EPA is investigating the potential for developing test protocols which predict the effects of chemical substances on selected ecological parameters, indicative of interspecific interactions, community dynamics, and ecosystem functions. Streamlined protocols are necessary if consistent results are to be expected among different laboratories. Unfortunately, the state of the art of ecotoxicology does not allow the choice of appropriate tests to be made easily. As a result, EPA has enlisted the aid of the Environmental Sciences Division (ESD), Oak Ridge National Laboratory (ORNL); the Council on Environmental Quality (CEQ); and the National Research Council (NRC) in its effort to determine the importance of including such tests in hazard assessment processes and to identify suitable extant tests and those most amenable to laboratory test development.

Three major efforts comprise the investigation initiated by EPA: (1) a review of laboratory test methods that predict ecological effects on interspecific interactions and ecosystem properties and of ecological parameters most amenable for laboratory test development; (2) an evaluation of their potential utility to the hazard identification and risk assessment processes of TSCA; and (3) development of recommendations and criteria that might be used to advance the state of applied ecological science in toxicological assessment. The CEQ contracted the NRC to establish a National Academy of Sciences (NAS) Committee of experts to perform the last task. The first two tasks have been performed by ESD, ORNL, under an Interagency Agreement between EPA and the Department of Energy (DOE). Results of the ORNL review and evaluation are contained in this report. The NAS report (NAS 1981) will be available in early 1981.

1.2 Scope and Organization

This report provides a review of tests for measuring aquatic and terrestrial population interactions and ecosystem properties in laboratory systems. Little information is available on techniques developed or used specifically to predict the effects of chemicals on ecological systems. Nevertheless, tests that might be considered are discussed in terms of their potential for use in this area. The criteria used to evaluate this potential include whether or not the tests are simple, rapid, reproducible, relatively inexpensive, unequivocal, sensitive, socially and economically relevant, and predictive. The extent of experience with and development of each test as well as the generalizability of test results were also considered. These criteria, which are necessary considerations for effective implementation of TSCA testing requirements, are defined in Section 1.4.

The general problems encountered in toxicology testing processes (i.e., selecting the appropriate dose, interpreting dose response, or choosing the best test species) intentionally are not discussed in this report. These problems are not unique to multispecies test procedures. Choices will depend to some extent on the environmental characteristics of each chemical, the expected release to the environment, and the potential for exposure. Criteria for evaluating these issues must be determined and established while tests are being developed and standardized.

Many resources were used to gather information, including the ORNL Ecological Sciences Information Center, workshops, and ESD staff scientists. The review of testing protocols was initiated by machine and manual searching for information published in scientific literature on (1) procedures used to measure changes in population dynamics such as competition, predation, parasitism, herbivory, and symbiosis and (2) ecosystem processes such as primary production, nutrient cycling, community metabolism, and litter decomposition. In addition, a series of six workshops on ecotoxicological test systems was conducted by the ESD staff to bring together investigators presently working with aquatic or terrestrial laboratory test systems. The intent of these workshops was to ensure that every available test potentially usable in a standardized ecological effects testing scheme would be identified and considered. The topics of the workshops were: Assessment and Policy Requirements of Ecological Toxicity Testing Protocols, Mathematical Models Useful in Toxicity Assessment, Methods for Measuring Effects of Chemicals on Terrestrial Ecosystem Properties, Methods for Measuring Effects of Chemicals on Aquatic Ecosystem Properties, Methods for Measuring Effects of Chemicals on

Terrestrial Population Interactions, and Methods for Measuring Effects of Chemicals on Aquatic Population Interactions. The results of these workshops will be published as a single ORNL/EPA report (Hammons, 1981). Other valuable resources were the many scientists at ORNL who were available for consultation, document review, and workshop participation and whose data files were made available for our perusal.

This report is organized into three sections: (1) aquatic population interactions and ecosystem properties, (2) terrestrial population interactions and ecosystem properties, and (3) mathematical models. A brief discussion of categories of models is included because models are recognized as potential tools for identifying and assessing environmental hazards.

Many published documents describing laboratory test systems were reviewed by the authors, and many investigators were contacted personally, but to minimize the time required to complete this project, no attempt was made to provide detailed methodologies or discussions of the results of all the tests considered. Nevertheless, examples of the different types of tests discussed in this report are cited throughout the text, and a complete bibliography is attached (Appendixes C and D) for the reader who is interested in obtaining more detailed information. Summary tables (Appendixes A and B) are also used to present additional details about the most significant aspects of specific tests.

1.3 Constraints

As expected, relatively few laboratory tests for predicting the effects of chemicals on interspecific interactions, community dynamics, or ecosystem properties exist. In addition, the understanding of community and ecosystem responses to perturbations is limited. This limited knowledge in basic ecology makes it impossible at present to recommend with certainty tests useful for successfully predicting adverse ecological effects resulting from exposure to chemical substances. It is important for the development of adequate hazard assessment tools to establish by continued research into the mechanisms of communities and ecosystems: (1) the limits to which these systems can be taken before recovery is no longer possible, (2) the measurable parameters or "symptoms" indicative of adverse effects, and (3) the generality of these symptoms among other communities and ecosystems.

The tests recommended in this report are considered to have the best potential for use under the TSCA based on the present state of the knowledge of ecotoxicological testing. As indicated throughout this report, more information is needed in many areas of ecological science before unequivocal conclusions can be reached concerning appropriate laboratory tests for predicting the ecological effects of chemical substances.

1.4 Criteria to Be Met for a Standardized Test

This report was prepared in the context of a general, tiered testing scheme for hazard assessment. Such a scheme provides for different levels or stages of testing which progressively become more complex and more definitive as positive results from one level trigger decisions to proceed to the next higher level.

Several criteria were determined by EPA and ESD to be important in selecting ecotoxicological tests for development and standardization for use in a hazard assessment scheme. These criteria were applied to the test systems reviewed for this report in a qualitative manner based on the scientific judgment of the authors and the input received from the many researchers who participated in the workshop series. Several of the criteria were applied differently, depending on the level of testing that was considered. For example, although cost should always be minimized, it would be expected to increase with increasing complexity of the test system used. Sufficient information was not always available to apply all of the criteria to all of the tests.

The following list provides definitions of the criteria as they were used in evaluating the tests selected for inclusion in this report:

Cost per Test - The total cost of completing a test for a single chemical assuming that the facilities are already available.

Documentation - The extent to which the behavior of a laboratory system (not necessarily toxicological) has been investigated and reported.

Generality - The usefulness of the test in predicting the responses of a variety of interspecific interactions or ecosystems and their major components.

Rapidity - The total amount of time required to complete a test assuming that facilities already exist.

Realism - The ability to unambiguously interpret the response of the test system in terms of responses of real ecosystems.

Rejection Standards - Defined criteria for rejecting test results--ranging from informal or common-sense criteria (e.g., many controls die) to a complete and well-defined set of criteria (e.g., more than 10% of controls fail to achieve a weight of 20 g).

Replicability - The variance in response within an experiment among individual units of a test system.

Reproducibility - The ability of a test to produce common results in different laboratories.

Sensitivity - The ability of a test to produce measurable responses at low doses of test chemicals.

Social Relevance - The value to society, direct or indirect, of the response measured. The value may be economic, aesthetic, or indirectly related to human health and welfare.

Standardization - The definition of conditions and components of a test system to allow different laboratories to obtain similar results from a test.

Statistical Basis - Accepted statistical criteria for detecting and interpreting responses of the test system.

Training-Expertise Requirements - The extent to which use of a test may be limited by requirements for higher education, specialized training, or expertise.

Validity - The extent to which the responses of a test system are known to reflect responses in the field.

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SECTION 2

CONCLUSIONS AND RECOMMENDATIONS

2.1 Aquatic Test Systems

We have surveyed the recent ecological and toxicological literature for reports of laboratory techniques for measuring the effects of chemicals on interactions between aquatic organisms. Interactions considered in this survey included interspecific competition, predation, parasitism, grazing (herbivory), and symbiosis. We found few relevant studies pertaining to parasitism, grazing, or symbiosis. However, a variety of techniques are available for testing chemical effects on competition and predation. A few of these techniques appear to be quite amenable for standardization and routine use--that is, they are relatively simple, rapid, economical, and reproducible.

We have also surveyed test methods for chemical effects on whole ecosystems. Ecosystem-level phenomena, such as energy flow, nutrient cycling, and homeostasis, result from interactions among ecosystem components, but the mechanisms involved are not completely understood. Effects of chemicals on ecosystem properties are therefore not predictable from results of single-species toxicity tests. Very little is known about the sensitivity of ecosystem properties to toxic chemicals. Furthermore, the complex network of interactions occurring in an ecosystem can cause chemical effects on one species to affect other ecosystem components in unpredictable ways. Because all populations in nature are parts of whole ecosystems, there is a clear need for methods of testing chemicals for ecosystem-level effects.

Very few aquatic multispecies test systems have been developed specifically for chemical hazard assessment, but several have been refined to the point that protocols could be formulated and tested with a variety of chemical types (Sect. 2.1.1). Other aquatic test systems are potentially usable for chemical hazard assessment, but require further research before standard procedures can be specified (Sect. 2.1.2). The true merits, if any, of all of these systems will be revealed only through practical experience. Moreover, effective use of laboratory test systems to predict chemical effects on aquatic population interactions and ecosystem properties will depend on advances in our basic understanding of the structure and function of aquatic ecosystems. Until such advances are forthcoming, no hazard assessment protocol at any level of biological organization can be considered truly "validated."

2.1.1 Available in the Near Future

(1) Algal competition. Algae are more sensitive to toxic chemicals when competitors are present than in pure culture (Fielding

and Russell 1976; Fisher et al. 1974; Kindig 1979; Mosser et al. 1972). Algal competition tests such as those of Mosser et al. (1972) and Fisher et al. (1974) are simple, inexpensive, rapid (1 to 2 weeks), easily standardized, and ecologically meaningful. Developmental needs include selection of appropriate species pairs, comparison of batch vs. continuous culture techniques, and standardization of experimental conditions. The ecological significance of alterations in phytoplankton community structure must be documented. Algal competition experiments are discussed in Section 3.1.1.

(2) Predation by fish. Predator-prey systems incorporating fish as predators and either fish or shrimp as prey are ready for standardization as hazard assessment protocols. Various options for the design of fish predation tests are discussed in Sections 3.2.4 and 3.2.5. Several experimental approaches have been used for measuring chemical effects, but without comparative data on specific compounds in different test systems, it is impossible to recommend any particular system for further development. Rather, the effects of major design options on the sensitivity, reproducibility, and efficiency of chemical effects tests should be investigated.

(3) Mixed flask cultures. Mixed cultures of bacteria, algae, protozoa, and zooplankton have been found to exhibit certain characteristics common to all ecosystems and could be used as ecosystem-level "white rats" for screening purposes. These abstract model ecosystems are small, easily replicated, and technically simple to operate. The major questions remaining to be resolved are: (a) are ecosystem-level properties more sensitive to chemicals than conventional bioassay organisms, and (b) are rankings generated by these systems different from rankings produced by conventional tests? If the answer to either question is affirmative, then mixed flask cultures should be included early in the chemical hazard assessment testing sequence. Factors to be considered in the design of these systems are discussed in Section 3.6.3 (1).

(4) Periphyton communities. Periphyton communities, which are found in nearly every aquatic habitat, exhibit all the major ecosystem functions. These communities grow well in laboratory systems; they are stable, replicable, biologically complex, and easily handled. Periphyton community structure has been widely used as an indicator of aquatic pollution, and chemical effects on periphyton community function have been observed in chronic experiments (Rodgers et al. 1980). Unlike the other test systems recommended for development in the near future, standardization of periphyton systems for chemical hazard assessment has not been attempted. However, the reviewer sees no serious methodological obstacles to the development of a periphyton community assay and recommends that research be initiated towards that objective [Section 3.6.3 (2)].

(5) Sediment cores. The technique of extracting sediment cores overlaid with water for study in the laboratory has been widely used by ecologists. If cores are maintained at ambient temperatures, with aeration and mixing of the water to simulate natural conditions, ecological processes and effects of chemicals can be examined over extended periods of time. The approach is essentially identical for studies in hypolimnetic, littoral, or coastal marine environments. The sediment core technique could be applied at almost any level of a hazard assessment scheme. Simple static systems are amenable to short-term tests of chemical effects, whereas more complex semi-continuous flow systems are suitable for long-term studies. An outline for a chemical testing protocol using sediment cores was formulated at the Workshop on Methods for Measuring Effects of Chemicals on Aquatic Ecosystem Properties held in conjunction with this project (Giddings 1981). This protocol, or one like it, should be refined and tested with a variety of chemicals. Relevant features of sediment core systems are discussed in Section 3.6.3(3).

(6) Pond microcosms. Naturally derived pond microcosms are structurally and functionally realistic representations of natural ponds. These model ecosystems are quite simple to assemble and to use for chemical effects studies, and a proposed pond microcosm protocol has been published (Harris et al. 1980). The next step in the development of these systems for chemical testing should be identification of the most sensitive and informative responses to be measured. The best use of pond microcosms in hazard assessment would be for confirmation and refinement of predictions based on simpler laboratory tests. At least one major chemical manufacturer (Monsanto) includes pond microcosms in the advanced stages of its hazard assessment program (Gledhill and Saeger 1979). Pond microcosm research is reviewed in Section 3.6.3(5).

2.1.2 Recommended for Research and Development

(1) Zooplankton-zooplankton predation tests. Most predator-prey studies with zooplankton have used the population approach in which groups of prey animals are exposed to a predator for a specified period of time, and the survivors of the prey population are counted. These experiments are simple and rapid and could easily be adapted to toxicity testing. Many zooplankton species are easily cultured, and large reproductive populations can be maintained in static aquaria. Predation tests can be conducted in small, static systems. Experiments can be completed in 8 h or less, and the surviving prey can be preserved to be enumerated later. Because zooplankton are nonvisual predators, lighting is not a critical factor, and experiments can be conducted in darkness. Learning, social interactions, and disturbances caused by observers are much less important in zooplankton-zooplankton systems than in fish systems. The sensitivity of zooplankton predation to chemicals is unknown. Replicability of zooplankton-zooplankton systems is probably good. These systems are discussed in Section 3.2.2.

(2) Fish-zooplankton predation tests. Many fish are obligate or facultative planktivores during at least part of their lives. The quality and quantity of available prey and the ability of fish to locate and capture food organisms are important factors in controlling fish productivity and in determining which fish species will succeed in a particular environment. Field studies have shown that selective predation by planktivorous fish can dramatically alter the species composition of the zooplankton community.

Fish-zooplankton predation tests are more complicated than tests with zooplankton predators. Fish cultures require more space than zooplankton cultures, and continuous flow systems are necessary for most species. Likewise, predation studies involving fish generally require large volumes and/or continuous flow. Lighting conditions and background must be carefully controlled to ensure repeatable results with these visual predators. Effects of learning, social behavior, and unintentional disturbances are more likely to occur with fish than with zooplankton predators. All of these factors imply that fish-zooplankton systems would be less amenable to chemical hazard assessment than zooplankton-zooplankton systems. However, experiments with fish might be faster than zooplankton predation tests since fish consume more prey in a given time than do zooplankton.

Because of the social and economic importance of many planktivorous fish, an attempt should be made to develop an efficient fish-zooplankton test system. The problems discussed above and in Section 3.2.3 indicate that test procedures would have to be specified in considerable detail, but the problems are not insurmountable in developing a protocol.

(3) Parasitism. It is widely recognized that the incidence of parasitism or disease in a population is determined partially by the physiological state of the host organism and that various environmental stressing agents can reduce the host's resistance to infection (Snieszko 1974; Wedemeyer 1970). However, only one example was found of an experiment specifically designed to measure chemically induced susceptibility to parasitism (Couch and Courtney 1977). Since the effects of chemicals (in this case, drugs) on parasitism and disease are the subjects of clinical parasitology, it is recommended that the literature of this field be surveyed to evaluate the possibility of developing a hazard assessment protocol.

(4) Zooplankton-algae grazing tests. Grazing by zooplankton on phytoplankton is recognized as an important component of ecosystem energy flow and nutrient cycling and as a possible determinant of plankton community structure, but it has received little attention in environmental toxicology. One reason for this is that methods for measuring plankton grazing rates, either in situ or in the laboratory, are still poorly developed. A phytoplankton-zooplankton hazard assessment test would be essentially a single-species bioassay, with zooplankton grazing rate as the measured response. Inert particles

could be (and often are) substituted for algae in this type of test without changing the nature of the experiment significantly. The sensitivity of zooplankton grazing to chemical stress is not known and should be investigated.

(5) Pelagic microcosms. Simulation of marine and freshwater pelagic (open-water) ecosystems in laboratory microcosms has been attempted at the EPA Environmental Research Laboratory at Narragansett, Rhode Island (Perez et al. 1977) and at the Lawrence Berkeley Laboratory (Harte et al. 1978, 1980). Pelagic ecosystems are dominated by physical processes such as turbulence and advection that are difficult to scale down to a laboratory system. However, by directing careful attention to simulation of natural physical conditions, it is possible to reproduce many features of pelagic ecosystems in the laboratory. In their current state of development, pelagic microcosms are useful tools for basic research and some special applications, but they are not yet ready for standardization as TSCA hazard assessment protocols. Further research should concentrate on measurements of ecosystem properties rather than taxonomic structure of pelagic systems. Given several more years of research, it is possible that a streamlined protocol will emerge for chemical hazard assessment. Pelagic microcosms are discussed in detail in Section 3.6.3 (4).

(6) Model streams. Streams are, in the opinion of Warren and Davis (1971), "among the most difficult freshwater systems to model." Participants in the Workshop on Methods for Measuring Effects of Chemicals on Aquatic Ecosystem Properties (Giddings 1981) concluded that simple laboratory recirculating streams come closest to satisfying the operational criteria (simplicity, rapidity, reproducibility, low expense) for a TSCA hazard assessment tool. However, the same systems that are most amenable for routine chemical hazard assessment may be the least generalizable to natural ecosystems. Small recirculating model streams lack the openness that is the distinctive feature of stream ecosystems; only larger, open systems are enough like natural streams to permit reliable predictions. Even with larger model streams, doubts about ecological realism were expressed by the participants in the Workshop (Giddings 1980). While potentially useful in many areas of applied and basic ecological research, model streams are not yet suitable for chemical hazard assessment under TSCA. With further refinement, they might be used in advanced stages of testing when transport and fate have been fully characterized and probable ecological effects have been carefully defined. Model streams are discussed in Section 3.6.3 (6).

2.2 Terrestrial Test Systems

Multispecies test systems are needed to test effects on system properties that are not present in single species systems because (1) emergent and collective properties of ecosystems cannot be tested in single species systems, (2) single organisms and populations do not necessarily respond realistically in isolation, and (3) the properties of chemicals can be changed by various ecosystem components. However, terrestrial ecotoxicology has been largely concerned with the transport, accumulation, and degradation of toxicants; this activity generates estimates of environmental concentrations, the results of which are interpreted according to the responses of single species. Ecosystem-level responses have been studied much less commonly, and most of this work has been done with systems that only include soil and associated microbiota. Only these systems are sufficiently developed for use in testing effects on ecosystem properties. The responses of more complex "microcosms" are not yet interpretable in terms of either their internal responses or their relevance to field responses, but results are sufficiently promising to justify further research and development.

Little work has been done on the toxicology of population interactions. It is not clear whether (1) species associations respond to chemicals as a unit, (2) the effects of chemicals on a species are qualitatively affected in any regular way by the presence of a second species, or (3) the presence of a second species simply has a quantitative effect on the response of the first species. A second major issue is generality--for example, which responses, if any, of a test system using predation by the parasitoid *Encarsia formosa* on the whitefly *Trialeurodes vaporariorum* are generally applicable to hymenopteran predators and homopteran prey, insect predators and prey, or to all predation. Answers to these types of questions are central to the design of a test program for population interactions because they indicate what parameters should be measured and which and how many species associations must be tested.

2.2.1 Available in the Near Future

Because terrestrial ecological toxicology has been a relatively neglected field, only a few potential test systems are available for use in the near future. In addition to the problems identified for each test, there are some common developmental problems. First, a set of standard reference test chemicals must be identified and used in test development and as positive controls for test use. Second, the responses of a test protocol must be validated by field experiments. Third, the ability of a test protocol to give consistent results must be confirmed by use in several laboratories.

(1) *Soil*. The best developed multispecies test system is a simple test for CO_2 production and nitrogen mineralization by natural soil microbial communities [Sect. 4.2.5(1)]. This type of test is relatively rapid, inexpensive, and easily performed. A tentative protocol for this test, similar to the one developed by the ORNL workshop participants (Suter 1981b), should undergo confirmatory testing to determine the effects of soil type and substrate amendments on standard reference chemicals. Studies to determine the optimum number of replicates, amount of soil per replicate, and sampling

schedule could be conducted concurrently. Because this system, as proposed, requires 2 weeks and is not apparently sensitive [Sect. 4.2.1(4)], it does not appear to be useful as a screening test, but it could be used relatively early in the hazard assessment process.

(2) Legume-rhizobia. A test for effects on this symbiotic relationship should be developed using a domestic legume, commercial innoculum, and greenhouse conditions [Sect. 4.1.5(2) and Suter 1980a]. Test development should include examination of the effects of soil type, legume and Rhizobium species, and parameters measured on test performance. This test should be easy to perform, relatively inexpensive, and require less than a month to complete. While it does not appear suitable for screening, it could be used early in the testing scheme.

(3) Mycorrhizae. Tests for effects of chemicals on the symbiosis of flowering plants with endo-and ectomycorrhizae should be developed [Sect. 4.1.5(3)]. Test development should include examination of the effects on test performance of soil type, plant and fungus species, and parameters measured. While these tests appear to be reasonably inexpensive and easy to perform, they would probably not be used early in a testing scheme because they require approximately 3 months for completion.

2.2.2 Recommended for Research and Development

(1) Population interactions. Because of the absence of toxicological experience with population interactions other than the two already listed (Sect. 2.2.1), there is no strong basis for selecting specific systems or even for prescribing the necessary number of categories of tests. However, on the basis of perceived importance, feasibility, and ability to represent real systems, we consider the following potential test systems to be good candidates:

Grass-legume competition [Sect. 4.1.1(2)]
Homopteran-plant herbivory [Sect. 4.1.2(1)]
Lepidopteran-plant herbivory [Sect. 4.1.2(2)]
Parasitoid-homopteran predation [Sect. 4.1.3(2)]
Ladybird-homopteran predation [Sect. 4.1.3(2)]
Mite-mite predation [Sect. 4.1.3(2)]

Other systems are highly developed and easily implemented, but are not felt to be realistic or representative. These systems can aid in the development of population interaction tests by providing relatively quick and inexpensive checks of the generality of responses observed in the more realistic test systems. This category includes:

Drosophila competition [4.1.1(3)]
Tribolium competition [4.1.1(3)]
Housefly-blowfly competition [4.1.1(3)]
Parasitoid-grain moth predation [4.1.3(2)]
Parasitoid-fly predation [4.1.3(2)]

Because there is no empirical or theoretical basis for ranking systems within these groups, ranking should be conducted on the basis of the interests and qualifications of responding researchers.

(2) *Ecosystems*. More research and development should be performed on medium-sized soil core microcosms with soil covers of litter, herbaceous vegetation, and seedling trees (Sect. 4.2.5 and 4.2.6). These studies are needed to elucidate the importance of the different physical and biotic components to system response (Sect. 4.2.2) and the importance and representativeness of parameters measured in microcosms relative to whole-ecosystem responses (Sect. 4.2.1).

2.3 Mathematical Models

A variety of mathematical models and modeling methodologies appear potentially useful in hazard assessments conducted under TSCA. Possible uses include both predicting the effects of chemical substances on multipopulation systems and ecosystems and interpreting the results of microcosm experiments in terms of causal pathways. Most of these models and methodologies were developed as research tools and have never had practical applications. All require substantial development and testing before they can be reliably used in hazard assessments. Additional research above and beyond the development of specific models is required because of the fundamental differences between mathematical models and laboratory test systems. The number and identity of components included in a model, as well as the detail with which each component is modeled, can be designed to fit the specific needs of the problem at hand. Strategies for efficiently utilizing this versatility in hazard assessments need to be developed. Similar, and equally plausible, models of the same system can yield radically different predictions about the effects of chemical substances. For this reason, it is essential that efficient methods for evaluating the validity of model predictions and for selecting between alternative models be developed.

2.3.1 Available in the Near Future

(1) *Ecosystem simulation models*. A variety of ecosystem simulation models exist that could, with varying degrees of modification, be used to make predictions about the effects of chemical substances on ecosystems. Because of their relatively realistic representations of ecological processes, forest succession

models (Botkin et al. 1972; Shugart and West 1977), IBP biome models (e.g., Innis 1972; Park et al. 1975), and pesticide fate-and-effects models (e.g., Falco and Mulkey 1976) appear to be especially appropriate candidates.

(2) Generalized multipopulation models. These are simple, highly generalized models that can be rapidly and inexpensively tailored to fit any system of interacting populations, aquatic or terrestrial. Because physical, chemical, and biological processes are not represented in realistic detail, these models are thought to be more appropriate for screening of substances for potential effects than for detailed toxicant- or site-specific assessments (as might be required in connection with regulatory actions).

(3) Loop analysis and time-averaging. Loop analysis (Levins 1974; Lane and Levins 1977) and time-averaging (Levins 1979) are methods of analyzing the qualitative behavior of systems of coupled differential equations such as those employed in generalized multipopulation models. In addition to predicting responses of multipopulation systems to chemical substances, these methods can be used (a) to identify critical parameters that should be measured, (b) to identify system properties that enhance or reduce impacts, and (c) to analyze data obtained from microcosm experiments.

(4) Input-output analysis. Input-output analysis (Finn 1976; Hannon 1973; Lettenmaier and Richey 1978) is a method of econometric analysis that has been modefied for use in analyzing material budgets in ecosystems. Presently, its primary use is in deriving descriptive indices that summarize complex data relating to material cycling patterns. Changes in these indices may indicate system dysfunction caused by stress. Input-output analysis requires further development and testing before it can be used for predictive purposes.

(5) Population genetics models. The very large body of theory on population genetics can be applied to predicting the evolutionary responses of populations to chemical substances. Such applications have great potential value because populations in nature frequently evolve in response to exposure to chemical substances (e.g., pesticides and antibiotics). No other kind of model can predict these effects.

2.3.2 Recommended for Research and Development

(1) Ecosystem parameter handbook. Standard ecosystem simulation models, specially tailored for predicting the effects of chemical substances, and standard data sets are needed for representative terrestrial and aquatic environments. As an aid to model development, an ecosystem parameter handbook should be compiled. This handbook would include definitions and standard notations for parameters that are used in ecosystem models. It would also include a codification of

properties of ecosystems relevant to modeling (e.g., numbers of trophic levels and functional groups in different ecosystem types, relationships between primary and secondary production, and average numbers of prey species fed on by various predators).

(2) Model validation methods. Research on model validation methods is urgently needed to support the use of mathematical models in hazard assessments. Clearly, it is necessary to evaluate the reliability of any model that will be used as part of the basis for regulatory actions. Equally important, efficient methods for determining the relative merits of alternative models must be developed, because decision makers in contested proceedings are likely to be presented with different models, sponsored by different contesting parties, that make radically different predictions because radically different predictions can be made using different models. The technical basis for recommending the specific research projects necessary for developing operational model validation protocols does not presently exist. It is recommended that EPA develop contacts with researchers actively engaged in model validation studies to enlist their aid in developing a research program. A national or international conference on model validation would be a valuable first step.

(3) Theoretical studies. Theoretical studies using generalized multipopulation models, loop analysis, input-output analysis, and any other similar analytical methodologies should be performed to define the possible responses of systems to chemical substances. Examples of the kinds of results that could be obtained are the identification of (a) system properties that confer resilience or vulnerability to chemical substances and (b) conditions under which sublethal exposures to chemical substances can cause destabilization of competitive or predator-prey systems. Results of such studies, which can be conducted relatively rapidly and inexpensively, would suggest processes that should be incorporated in more complex models and hypotheses that should be tested using ecosystem simulation models, microcosm studies, and field studies.

(4) Strategy for model selection and application. Regardless of how many and what kinds of models are available, an overall strategy for selecting and applying models will be required to use models productively as part of the hazard assessment process. As part of this strategy, a flowchart decision tree should be developed as an aid in identifying the best model(s) for any given assessment problem. Because development of this strategy will require intimate knowledge of the hazard assessment process and the overall procedures for implementing TSCA, active participation by the Office of Toxic Substances will be necessary.

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LABORATORY TESTS FOR CHEMICAL EFFECTS ON AQUATIC POPULATION INTERACTIONS AND ECOSYSTEM PROPERTIES

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SECTION 3

LABORATORY TESTS FOR CHEMICAL EFFECTS ON AQUATIC POPULATION INTERACTIONS AND ECOSYSTEM PROPERTIES

This section presents the results of a survey to identify methods for measuring chemical effects on aquatic population interactions and whole ecosystems. These methods are evaluated in the context of a tiered hazard assessment scheme (Cairns 1980; Hushon et al. 1979). In such a scheme, chemicals are first subjected to a battery of simple, rapid tests aimed at identifying those chemicals that might be hazardous to the environment. Chemicals that are indicated to be potentially hazardous are tested further to better define the effects that might occur and to establish the concentration ranges likely to produce those effects. If the concentration that produces adverse effects is close to the expected environmental concentration, the chemical is tested under more realistic conditions to confirm the earlier results and to predict the ecological impacts in as much detail as possible.

Tests to be used early in the assessment process must be highly _sensitive_, since the objective is to produce no false negatives (Hushon et al. 1979). Because these early tests will be applied to hundreds or thousands of chemicals, they must also be _rapid_, _inexpensive_, _replicable_, and _readily standardized_ for use by different laboratories. Tests for confirmation and prediction can be more expensive and time-consuming, since few chemicals will reach this stage of the assessment scheme; however, these tests must include as much _ecological realism_ as possible so that actual effects may be reliably predicted. Tests used in the intermediate stages of the assessment scheme are designed to compromise between realism on the one hand and sensitivity, rapidity, replicability, low cost, and standardizability on the other. Most of the tests reviewed are most suitable for the intermediate and advanced stages of hazard assessment, but a few might be incorporated into the initial battery.

Few aquatic multispecies test systems have yet been developed or adapted for chemical hazard assessment. Without a great deal more practical experience with chemical effects testing above the population level, it will be impossible to determine which types of tests will be most useful. Development of chemical hazard assessment protocols should draw on the entire body of ecological experience rather than focusing too narrowly on a particular published procedure. Therefore, this review can only indicate general approaches that appear to be fruitful, without recommending specific procedures to be followed. Where alternative strategies exist for conducting a given type of experiment, major issues are discussed which must be resolved before a standard method can be selected.

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3.1 Competition

Competition has been defined as an interaction between two species in which each population adversely affects the other in the struggle for limiting resources (Odum 1971). Competition is not a series of discrete events, like predation, but rather is manifested over generations in the history of a population. Therefore, laboratory studies of competition are usually conducted with short-lived organisms such as bacteria, algae, and zooplankton.

Many organisms are more sensitive to toxic chemicals when competitors are present than in pure cultures (Fielding and Russell 1976; Fisher et al. 1974; Kindig 1979; Mosser et al. 1972). Chemical effects on competition are generally interpreted as effects on the abilities of organisms to take up, assimilate, or store a limiting resource. If competing species are affected by a chemical in different degrees, the normal competitive dominance under a given set of conditions may be altered or reversed. On a community level, this results in changes in the relative abundance of species, with or without a change in the total biomass or overall activity of the community (May 1973; O'Neill and Giddings 1979).

The effects of a chemical on a group of competing species depend on the environmental conditions and on which species are present (Fielding and Russell 1976). The behavior of any species, including its abundance and distribution in space and time, can vary tremendously in the presence of different competitors (O'Neill and Giddings 1979). Thus, the results of a competition experiment with two species do not indicate what would have occurred if a third species had been involved. Competition experiments have been used primarily to elucidate the mechanisms of competition and to validate ecological theories, rather than to predict the course of events in nature.

Because they are (1) extremely sensitive and (2) nonpredictive, competition experiments are most applicable in the first or intermediate levels of the hazard assessment sequence. Zooplankton competition experiments reported in literature range from 6 to 100 weeks in duration, so their utility for testing large numbers of chemicals is doubtful. Experiments with algae can be completed in as little as 4 days, and bacterial experiments may be even shorter. Because only one example of a bacterial competition experiment (Hansen and Hubbell 1980) was found in our literature review, we have focused on algae as logical subjects of tests for chemical effects on competition.

3.1.1 Algal Competition Experiments

Competition can be extremely important in structuring algal communities (O'Neill and Giddings 1979). Shifts in algal dominance may have repercussions on the quality and abundance of animal life in an aquatic ecosystem because some algal species are not easily ingested or are of greater nutritional value to consumers than are others (see references cited in Mosser et al. 1972). Assessment of the true ecological significance of alterations in algal community structure should be an objective of future research.

Of all the numerous published studies of algal competition (Appendix A), those by Mosser et al. (1972) and Fisher et al. (1974) are perhaps the best demonstrations of the ability of algal systems to reveal effects at very low chemical concentrations. These experiments involved the marine diatom Thalassiosira pseudonana and the marine green alga Dunaliella tertiolecta. The growth of T. pseudonana in pure batch culture was inhibited by polychlorinated biphenyl (PCB) at 25 µg/L, but not at 10 µg/L or less. D. tertiolecta in pure culture was unaffected by 25 µg/L. When grown together in batch culture with no PCB, T. pseudonana attained densities 8 or 9 times as high as D. tertiolecta. However, when PCB at 1 µg/L was included in the medium, the growth of T. pseudonana was slightly reduced and that of D. tertiolecta was substantially increased, resulting in T. pseudonana to D. tertiolecta cell ratios of only about 2 to 1 (Mosser et al. 1972). The authors concluded that the diatom normally stripped the nutrients from the medium before the green alga could achieve much growth. PCB impaired the diatom's nutrient uptake capacity and thus permitted the green alga, which was unaffected, to reach higher population densities.

In a subsequent study, Fisher et al. (1974) compared the effects of PCB in batch and continuous cultures of the same two species. PCB at 0.1 µg/L did not affect the outcome of competition in mixed batch cultures, nor did it affect either species growing alone in continuous culture. In mixed continuous culture, PCB reduced the proportion of T. pseudonana to 50% of the total cells, as compared to control proportions of over 90%. When natural phytoplankton communities dominated by T. pseudonana and two other diatom species were tested in similar continuous culture experiments, the same effect on T. pseudonana was observed as in the two-species experiments. The PCB concentration of 0.1 µg/L that produced this effect was at least two orders of magnitude below the concentration that inhibited pure batch cultures of T. pseudonana.

Continuous cultures are appropriate for algal competition experiments for several reasons (Fisher et al. 1974). In a continuous culture, resources are always limiting; therefore, competition is always occurring. Batch cultures, however, do not become nutrient-limited until they reach the senescent phase. Continuous cultures can be maintained in the active growth phase for longer periods than batch cultures, thus allowing competitive displacement to take place. The greater sensitivity of continuous cultures, compared to batch cultures, derives from these two factors. Continuous cultures are certainly more representative of most natural growth situations. On the other hand, batch cultures are technically simpler (although analytically more complex) than continuous cultures. An effort should be made to assess the relative cost, efficiency, and sensitivity to chemicals of these two kinds of competition tests.

3.1.2 Conclusions and Recommendations

The studies of Fisher et al. (1974) and Mosser et al. (1972) are examples of how algal competition experiments could be applied in chemical hazard assessment. Other competition experiments are described in Appendix A. Because these systems are relatively simple and extremely sensitive to chemicals, they should be developed into a TSCA hazard assessment protocol. A systematic search for suitable species pairs (freshwater and marine) should be undertaken, basing the final selection on ease of culture, predictability of response, sensitivity to chemicals, and ecological relevance. Optimal experimental conditions can then be established, and the system can undergo the validation and interlaboratory testing sequence necessary for all standard methods.

3.2 Predation

The principal mechanism by which chemicals (and other types of stress) have been observed to influence predator-prey interactions is through behavioral alterations in the prey. These behavioral changes often make the prey more conspicuous to predators (e.g., increased activity, erratic movement, failure to seek shelter) or reduce their ability to avoid capture once detected (e.g., sluggishness, slowed swimming speed, reduced stamina). Most published experiments on chemical effects on predator-prey interactions, therefore, have been essentially behavioral studies.

Behavioral effects of chemicals are generally the most sensitive type of sublethal response. Furthermore, natural predators are frequently capable of discerning behavioral abnormalities in their prey even when the abnormalities are not obvious to a human observer. Therefore, predator-prey interactions should be affected by chemicals at lower concentrations than many biological responses measured in conventional toxicity tests. Indeed, many of the studies reviewed in this section demonstrated predator-prey effects at concentrations orders of magnitude below the lethal level. The apparent sensitivity of predator-prey interactions is the major justification for their inclusion in a hazard assessment program.

However, because chemical effects on predation derive primarily from behavioral alterations in the prey, the response of any particular predator-prey combination may not be readily generalizable to other species pairs. For example, stress-induced hyperactivity can make mosquito fish more susceptible to predation by largemouth bass (Goodyear 1972), but less susceptible to predation by bowfin, which prefer slow-moving prey (Herting and Witt 1967). Current knowledge of critical factors in predator-prey interactions does not allow us to select a small set of species pairs upon which to base general conclusions about chemical effects on predation. An effect observed in one situation serves only to indicate the potential for effects on other predator-prey interactions, but the magnitude, direction, or even occurrence of effects on other species pairs cannot be accurately predicted.

Effects observed in most laboratory predator-prey experiments are of no more value in predicting actual events in nature than conventional bioassay results. A multitude of physical, chemical, and ecological factors other than predation influence the distribution, abundance, and activities of species in natural ecosystems. As an obvious example, a population whose density is limited by intraspecific competition may be totally unaffected by changes in predation rates. To predict the effect of a chemical on natural populations from results of a predator-prey experiment, detailed information on the population dynamics of both species and on the trophic structure of the ecosystem would be needed at the very least.

High sensitivity, poor generalizability, and poor predictive power of predator-prey tests imply that they would be most useful in the early stages of a hazard assessment scheme. Methods used early in the testing sequence must be simple, inexpensive, and rapid since they will be applied to a large number of chemicals; they must also be well standardized so that consistent results can be achieved by different laboratories. Therefore, the experimental approaches evaluated below were selected from the many published techniques because of their efficiency and ease of standardization.

Many studies of predation are designed to measure specific components of a predator-prey interaction such as reactive distance, handling time, or capture success. An alternative approach is to enclose a predator with a population of prey and count the survivors. These two types of experiments can be labeled the "mechanistic approach" and the "population approach," respectively, for lack of better terms. It must be presumed that at least some mechanisms are more sensitive to chemical stress than the net survivorship of the population because various factors may compensate for changes in particular components of the interaction. To choose a hypothetical example, a chemical that produces hyperactivity in the prey might reduce the searching time of the predator, but may simultaneously make the prey more difficult to capture. The net effect on the predation rate might be small. Effects of chemicals on mechanisms might also be more generalizable to other species than effects on net population survival. To extend the above example, a chemical causing hyperactivity in one species would probably produce the same effects on related species, but the compensating effect (decreased capture success) would depend on specific behavioral characteristics of the predator and the prey; hence, the net outcome might be different with different species pairs. Focusing on a single component of the predator-prey interaction might make a test more sensitive and more generalizable, but omission of potential compensating effects would reduce the predictive power of the test compared to a test using the population approach.

The mechanistic and population approaches impose different demands on the investigator. Population experiments under reasonably realistic conditions take at least several hours and sometimes days or weeks. Mechanistic measurements are often completed in seconds or minutes. However, mechanistic measurements must be repeated many times to generate enough data for statistical analysis, while a carefully controlled population experiment might need to be performed only once or twice to achieve the same level of statistical confidence. Most mechanistic approaches require that an observer monitor the experiment continuously (e.g., to count attacks or captures or to measure handling time or reactive distance). A population experiment can be designed in such a way that only one count of surviving prey is necessary. Depending on the organisms involved, the survivors may even be preserved to be counted at the convenience of the experimenter. Therefore, one experimenter can conduct a number of population experiments at once, but mechanistic experiments have to be run separately. Because experience is lacking with either approach to chemical testing, neither is clearly preferable in every case.

In the population approach, treated and control prey may be offered to the predator simultaneously or in separate trials. Either strategy has certain advantages and disadvantages, as discussed in Sect. 3.2.5(2). With simultaneous exposure of two prey groups to the predator, some means of differentially marking the groups is necessary; this may be impossible with zooplankton. The experimental results are complicated by the continuously changing ratios of the two prey groups. The possibility of treated prey affecting the performance of control prey cannot be discounted, especially in experiments with schooling fish. However, when prey groups are presented separately, differences in predator performance may obscure treatment effects. Ideally, the same predator or group of predators should be tested with both treated and control prey so that variations among predators do not influence the results. Even with this precaution, the order in which prey groups are presented may be significant; learning in one trial may affect the outcome of the next. [This is possible even in protozoa (G. W. Salt, personal communication).] Another disadvantage of separate presentation is that more trials are required than when prey groups are presented simultaneously. A systematic investigation of these factors should be conducted before selecting either experimental design for chemical hazard assessment. It should be pointed out, however, that mixed groups of exposed and unexposed prey are probably unusual in nature.

3.2.1 Protozoa-Protozoa

Protozoa have been popular subjects for predation studies since the early experiments of Gause (1934; Gause et al. 1936). Salt (1967) offered two reasons why protozoa are well suited for such research: (1) "if there are any universal characteristics of predation they should be present in the simplest animals;" and (2) such characteristics should be more easily discernable in protozoa than in animals with sexes, life stages, and other complicating factors. Protozoa have therefore been used as model predators; the publications reviewed here did not consider the ecological significance, if any, of protozoan predation.

(1) Population dynamics experiments. The ciliates *Didinium nasutum* (a predator) and *Paramecium aurelia* or *P. caudatum* (prey) were selected by Gause (1934), and many of those who followed him, in studying predator-prey interactions among protozoa. Gause found that mixed cultures of these species were invariably short-lived. Growth of *Paramecium* populations allowed *Didinium* to increase. *Didinium* then drove the prey to extinction and subsequently starved. This simple predator-prey oscillation leading to extinction of prey was also observed by Luckinbill (1973, 1974) and by Veilleux (1979). As Salt (1974) pointed out, this phenomenon is "precisely what does not occur in nature." A great deal of theoretical and experimental work, including the studies reviewed below, has been directed towards identifying the critical factors permitting stable coexistence of protozoan predators and their prey.

Luckinbill (1973) reasoned that the predator-prey interaction might be stabilized if the frequency of predator-prey encounters could be reduced. He cultured *Didinium* and *Paramecium* together in a medium to which methyl cellulose had been added to slow the movements of both species. The medium was enriched with Cerophyl, a bacterial growth medium, inoculated with *Aerobacter aerogenes* as food for *Paramecium*. The cultures were started with 35 predators and 90 prey in 6 ml of medium. All the animals were removed and placed in fresh medium every 2 days. Without methyl cellulose, these cultures went through a typical predator-prey oscillation terminating in less than 10 h with the extinction of *Paramecium*. Methyl cellulose prolonged the interation; the cultures persisted through two to three oscillations over 16 days, and *Didinium* was the first to become extinct. Luckinbill found that the oscillations could be perpetuated by reducing the food supply to the prey (by reducing the Cerophyl concentration). With fewer bacteria, the *Paramecium* were undernourished at the peaks of their population density. *Didinium* feeding on these undernourished *Paramecium* reproduced more slowly than when feeding on healthy prey and were unable to completely eliminate the prey. These cultures (with methyl cellulose) went through seven stable oscillations in 32 days and were terminated voluntarily. Luckinbill concluded that coexistence of predator and prey was possible if two conditions were met: (1) the prey were able to reach low enough densities that the predator could not find them all, while still maintaining numbers that ensured the survival of the population; and (2) the prey were restricted in their growth by something other than predation (in this case, food).

Veilleux's (1979) methods were nearly identical to Luckinbill's method, with the following exceptions: (1) rather than transferring all the animals to fresh medium every 2 days, Veilleux replaced half the culture volume with fresh medium and did not remove any ciliates; and (2) the cultures were started with 15 *Didinium* and 45 *Paramecium*. Without methyl cellulose, these cultures became extinct without oscillations. With methyl cellulose in the medium, the experimental outcome depended on the Cerophyl concentration. At high Cerophyl concentrations, the prey eventually became extinct after a series of oscillations of increasing amplitude. At slightly lower Cerophyl concentrations, the predator became extinct. With still lower Cerophyl levels, the cultures reached stable oscillations. At the lowest Cerophyl concentrations, the *Paramecium* did not support the nutritional requirements of *Didinium*, and the latter became extinct. The conditions resulting in stable oscillations were the same as those in Luckinbill's study (1973).

Luckinbill (1974) attempted to produce stable cultures without methyl cellulose by increasing the culture volume. He reasoned that with a relatively large "arena" for the predator-prey interaction, the prey could reach low enough population densities to avoid capture by the predator while still maintaining an absolute population size sufficient to ensure their survival. He established cultures ranging from 0.1 mL to 1000 mL, each with initial densities of 20 *Paramecium* and 10 *Didinium* per milliliter. The cultures were observed under a dissecting microscope at 20-min intervals until no *Paramecium* could be found. None of the cultures attained stable oscillations, but their persistence increased from 2.8 h at 0.1 mL to 82 h at 1000 mL. Reducing the Cerophyl concentration prolonged the existence of large cultures, but did not stabilize them. In nature, the almost infinitely large "arena," coupled with possible food limitation of prey, may permit the coexistence of protozoan predators and prey (Luckinbill 1974). In the laboratory, coexistence has been achieved only in cultures with methyl cellulose.

(2) *Mechanistic studies*. Salt (1967, 1968, 1969, 1974) and Veilleux (1979) devised experiments to measure several other aspects of the predator-prey interaction among protozoa. Unlike the experiments described above, these mechanistic studies were not intended to perpetuate a predator-prey system, but rather to measure various components of the interaction over short time intervals. The experiments were conducted in 0.1-mL cultures, covered by a layer of paraffin oil to prevent evaporation (Salt 1967). Salt (1967) devised an automated system to photograph entire 0.1-mL drops periodically. The numbers of animals and, in some cases, their metabolic state could be determined with good accuracy by examining the film record under a

dissecting microscope. Salt's basic technique was to start a culture with two predators (Didinium nasutum, Amoeba proteus, or Woodruffia metabolica) and about 200 prey (Paramecium aurelia). No food was provided for the prey; prey were added to the cultures as needed to maintain the desired densities throughout an experiment. Each experiment was terminated when the predators reached a preselected density. Based on the counts derived from the film record, Salt calculated the generation times, feeding rates, and other characteristics of the predator. His primary objective was to examine variations in these parameters as a function of predator and prey densities. Veilleux (1979) used similar methods (generally in shorter experiments) to investigate the effects of methyl cellulose and Cerophyl concentrations.

The generation times of Woodruffia (Salt 1967), Amoeba (Salt 1968), and Didinium (Salt 1974; Veilleux 1979) were independent of predator and prey densities. The generation time of Didinium, however, was increased when the animals were feeding on undernourished Paramecium (Veilleux 1979). According to Salt (1969), Woodruffia cultured in the laboratory for 1000 to 1500 generations had longer generation times than members of the same species freshly collected from the field. He inferred that the animals had undergone genetic changes in the laboratory cultures and cautioned against using data from laboratory stocks to make quantitative predictions about wild populations.

The rate of food consumption by Didinium was shown to vary with the density of prey (Salt 1974; Veilleux 1979). The maximum feeding rate in Salt's experiments was about two prey per predator per hour; Veilleux (1979) measured up to 12 prey per predator per day. The discrepancy may reflect differences in Cerophyl concentrations in the cultures of Paramecium fed to the predators or the Didinium cultures used by the two investigators may have been genetically different. Because both authors omitted certain relevant information in their descriptions of methods, the discrepancy remains unresolved.

Another quantity measured in several of these studies was the number of prey consumed by one predator before fission occurred. Salt found this number to decrease with increasing predator density in cultures of Woodruffia (Salt 1967) and Amoeba (Salt 1968) and later concluded that the metabolic efficiency of these predators was greater at high densities (Salt 1979). Veilleux (1979) measured a three-fold variation in prey consumed per fission in Didinium over a range of Cerophyl concentrations.

For the most part, the connection between these mechanistic studies and the population dynamics experiments has not been made. In particular, the density-dependence of some components of the predator-prey interaction have yet to be assimilated into mechanistic population models.

(3) Evaluation. The social significance of nonpathogenic protozoa is nil, and the ecological significance of protozoan predators is not well known. The major advantages of protozoa as subjects for chemical effects tests are their small size and ease of culture. Protozoa tests are probably easier to standardize than tests with higher organisms, and no special equipment or skills are required. Counting protozoan populations, however, is tedious and could limit the number of tests that could be run in a given period of time. The suggestion that protozoa, by virtue of their simplicity, exhibit the essential features of all predator-prey phenomena (Salt 1967) is not entirely logical, and there is little evidence to support it. Protozoan predator-prey systems have little utility for chemical hazard assessment in their present state of development.

3.2.2 Zooplankton-Zooplankton*

The impact of predation on the composition of freshwater zooplankton communities has been extensively studied over the past two decades in field observations and laboratory experiments (Hall et al. 1976). The primary emphasis has been on vertebrate predators (see Sect. 3.2.3). Only recently have studies focused on the effects of invertebrate predators on zooplankton communities. Brooks and Dodson (1965) originally hypothesized that when vertebrate predation was low, the dominance of large zooplankton species was due to their ability to outcompete smaller species for a limited food supply. However, efforts to verify this hypothesis were inconclusive (Hall et al. 1976). Dodson (1974a) later proposed that small zooplankton are selectively reduced by invertebrate predators. Supportive evidence for this hypothesis has come from numerous field studies (Allan 1973; Anderson 1970; Confer and Cooley 1977; Dodson 1970, 1972; Lynch 1979; McQueen 1969; Sprules 1972). Other field studies have suggested that under the constant stress of invertebrate predation, individuals of the stressed populations undergo morphological changes (Dodson 1974b; Kerfoot 1975; O'Brien and Vinyard 1978; O'Brien and Schmidt 1979; O'Brien et al. 1979) or reproductive changes (Kerfoot 1974, 1977a) to reduce this predation. Laboratory studies that have attempted to test these hypotheses are the focus of this section. Although these studies were designed to examine individual predator-prey interactions, the techniques could be adapted for the testing of chemical substances for environmental effects.

Invertebrate predators such as the cladocerans *Leptodora* and *Polyphemus*, cyclopoid copepods, and certain calanoid copepods, and the phantom midge larvae *Chaoborus* are primarily nonvisual, grasping predators that depend to some extent on random contact for prey capture (Zaret 1975). Gerritsen and Strickler (1977) recognized four progressive stages of interaction for this type of predation: encounter, attack, capture, and ingestion. However, because of the small size of the animals, very little detailed information is available on these various stages.

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*This section was contributed by John D. Cooney, University of Tennessee.

(1) High-speed photography studies. Through the use of high-speed photography and constant observation under a dissecting microscope, Kerfoot (1977b, 1978) was able to document the predator-prey interaction between cyclopoid copepods of the genus *Cyclops* and the cladoceran *Bosmina longirostris*. Kerfoot found that cyclopoids can perceive objects at a distance of about 2 to 3 body lengths and that most attacks on prey occur within a single body length (about 1 to 2 mm). Zooplankton swimming speeds have also been measured by high-speed photography (Gerritsen 1978; Strickler 1977). Different instars and sexes of the same species may swim at different speeds. This is important because the probability of a planktonic animal encountering an invertebrate predator is determined in part by the animal's swimming speed. Acridine, a nitrogen-containing aromatic compound, has been observed to reduce the swimming speed of copepods (J.D. Cooney, unpublished data).

High-speed photography has also revealed that the predator's hunting strategy is important in determining the probability of encountering prey. Ambush predators, such as phantom midge larvae (*Chaoborus*), rest motionless in the water column and attack passing prey. For these animals, encounter probability is a function of prey speed. With predators that swim continuously, such as the calanoid copepod *Epischura*, encounter probability is relatively constant (Gerritsen 1978).

Studies such as these have provided useful information on predator-prey interactions. However, high-speed photography techniques are highly specialized and are not readily adaptable to general toxicity testing.

(2) Population experiments. Most predator-prey studies with zooplankton have used the population approach in which prey animals (or groups of prey of different sizes or species) are exposed to a predator for a specified period of time, and the survivors of the prey population are counted. Groups of prey without predators are sometimes included in these experiments as controls. Experiments may be as short as 6 to 8 h (Mullin 1979), or they may continue for several days with new prey added daily (Brandl and Fernando 1974; Confer 1971). The length of the experiments should be shorter than the reproductive period for the test animals because many predators eat their own young, which would bias the results. Many species of predators and prey have been studied. Cyclopoid copepods (e.g., *Mesocyclops* and *Cyclops*) are the most common predators, and cladocerans (e.g., *Bosmina* and *Ceriodaphnia*) or calanoid copepods (e.g., *Acartia* or *Diaptomus*) are typical experimental prey. A few studies (Brandl and Fernando 1978; Li and Li 1979) have used natural

prey communities. Similar techniques have been used to study predation by insect larvae (Akre and Johnson 1979; Gerritsen 1978; Thompson 1978).

In most of these studies, the experimental animals were obtained directly from field collections and then sorted in the laboratory, either by using a dissecting microscope or by passing the plankton sample through a series of sieves of various mesh sizes. These procedures are tedious and may injure the animals. Brandl and Fernando (1978) used a sieve to remove predators and then used a plankton splitter to subdivide the prey animals into control and test groups. Predators were then reintroduced at varying densities, and prey numbers were compared with control groups after 24 h.

Acclimation periods for experimental animals ranged from 6 h (Confer 1971) to one week (Kerfoot 1977). Standard acclimation periods are important to ensure the same nutritional status for predators in each test. Some investigators recommend starving predators for 24 h before testing (Akre and Johnson 1979; Gerritsen 1978; Kerfoot 1977; Li and Li 1979).

Containers most frequently used in testing were glass beakers, ranging in size from 50 to 4000 mL (Brandl and Fernando 1979; Confer 1971; Kerfoot 1977; Landry 1978; Mullin 1978). Li and Li (1979) used small Petri dishes, which facilitated observations under a dissecting microscope. Kerfoot (1977) found rectangular 10 L aquaria to be inadequate because prey animals would remain in the corners, where predators have difficulty feeding.

Studies that use field collections as a means of obtaining experimental animals are severely limited by temporal abundance of suitable predators and prey. Using zooplankton species for which culture methods have already been determined and life history parameters measured in the laboratory (e.g., _Diaptomus clavipes_, _Bosmina longirostris_, _Cyclops bicuspidatus thomasi_, _Cyclops versalis_) would be more efficient and would provide an abundance of experimental animals of the required sizes throughout the year. The use of laboratory animals would also reduce the inherent variability of results obtained using field-collected animals because laboratory populations could be homogeneous with respect to nutritional status.

(3) _Evaluation_. Zooplankton predator-prey experiments are simple and rapid and could be easily adapted to toxicity testing. Many zooplankton species are easily cultured, and large reproductive populations can be maintained in static aquaria. Their short lifespans and small size make it possible for many experiments to be conducted in limited space and time. Experiments can be completed in 8 h or less, and the surviving prey can be preserved to be enumerated later. Because zooplankton are nonvisual predators, lighting is not a critical factor, and experiments can be conducted in darkness. Learning, social interactions, and disturbances caused by observers

are much less important in zooplankton predation tests than in tests with fish (see Sects. 3.2.3, 3.2.4, and 3.2.5). Replicability of zooplankton-zooplankton systems is probably good. There are no reports of chemical effects studies on zooplankton predator-prey interactions.

3.2.3 Fish-Zooplankton

Many fish are obligate or facultative planktivores during at least part of their lives. The quality and quantity of available prey and the ability of fish to locate and capture food organisms are important factors in controlling fish productivity and in determining which fish species will succeed in a particular environment. Furthermore, several field studies have shown (Brooks and Dodson 1965; Dodson 1970; Galbraith 1967; Green 1967; Hall et al. 1970; Warshaw 1972; Wells 1970) that selective predation by planktivorous fish can dramatically alter the species composition of the zooplankton community. Brooks and Dodson (1965) hypothesized that fish alter zooplankton communities by preferentially consuming larger individuals. This suggestion prompted many investigations into the selective feeding habits of planktivorous fish and the mechanisms responsible for the observed food preferences. Effects of toxic chemicals or other environmental stresses have not been examined in this context, but some of the experimental techniques used to study fish-zooplankton interactions in the laboratory could be adapted for chemical hazard evaluation.

(1) Reactive distance. In a recent analysis of fish predation on zooplankton, O'Brien (1979) distinguished four phases of the interaction: location of prey by fish, followed by pursuit, attack, and capture. Because prey are small relative to predators, location of prey is usually the critical step in feeding. Most planktivorous fish are visual predators, and their ability to locate prey is influenced by prey size (Confer and Blades 1975a, b; Confer et al. 1978; Eggers 1977; Vinyard and O'Brien 1976; Ware 1972, 1973; Werner and Hall 1974), prey pigmentation (Confer et al. 1978; Eggers 1977; Ware 1973; Zaret 1972; Zaret and Kerfoot 1975), prey movement (Confer and Blades 1975a; Eggers 1977; Ware 1973), predator hunger (Confer et al. 1978), and light intensity (Confer et al. 1978; Eggers 1977; Vinyard and O'Brien 1976; Ware 1973).

The ability of a fish to locate zooplankton prey is commonly expressed in terms of reactive distance (RD)--the distance between predator and prey when the predator begins pursuit. Reactive distances have been measured in the laboratory by Confer and Blades (1975a, b), Confer et al. (1978), Vinyard and O'Brien (1976), Ware (1972, 1973), and Werner and Hall (1974). The methods used in these various experiments have much in common. In each case a starved fish is placed at one end of a long, narrow aquarium, and a prey is introduced at a distance beyond the fish's visual range. The point at which the fish begins to pursue the prey is observed, and the distance from that point to the prey is measured by a scale along one side of the aquarium. Distinguishing active pursuit from random searching is not always possible; Confer and Blades (1975a) reported discarding one-third of their observations for this reason, and the problem has undoubtedly occurred with other workers who simply did not report it.

A long, narrow aquarium is necessary so that RD can be accurately determined from the positions of predator and prey along one dimension. This introduces some artificiality into the predator-prey interaction since fish need only search in one direction. Confer et al. (1978) used a large aquarium and three observers to determine RD in three dimensions for lake trout (*Salvelinus namaycush*). They discovered that fish searching in three dimensions are not 100% efficient--that is, they overlook some prey within their visual range. These authors concluded that the actual volume searched by this fish is 50 to 70% less than would be estimated from the RD measured in a long, narrow tank. This factor would not affect comparisons of relative RD, but it would have to be considered in predicting absolute predation rates in nature.

The reactive distance of fish decreases as they become satiated (Confer et al. 1978). To eliminate this variable from experiments, fish are usually starved for at least 24 h before feeding trials. A single fish can be used for a number of trials in one experiment before satiation begins to reduce the RD. Bluegill (*Lepomis macrochirus*) 6.5 cm in length can consume more than 25 large *Daphnia magna* without affecting RD (Vinyard and O'Brien 1976), and 11-cm lake trout (*Salvelinus namaycush*) can eat 65 *D. magna* before RD begins to decline (Confer et al. 1978). A fish can be used for more than one experiment if a starvation period is allowed between experiments.

Not all fish are amenable to laboratory experimentation. Zaret (1972; Zaret and Kerfoot 1975) found that *Melaniris chagresi*, a planktivore from Gatun Lake, Panama, were extremely nervous in aquaria and could not be held in captivity for more than 10 days. Vinyard and O'Brien (1975) reported terminating some feeding sessions with bluegill (*Lepomis macrochirus*) when the fish became excited or distressed. Any fish used in predation studies must be conditioned to find and capture prey under experimental conditions. Introducing the prey without attracting or disturbing the fish may be difficult. Vinyard and O'Brien (1976) waited until the fish was facing the opposite direction before placing the prey into the aquarium. In other studies (O'Brien et al. 1976; Ware 1973), the aquarium was partitioned into a holding compartment and a feeding compartment. After the fish was placed in the holding compartment and activity normalized, the prey was positioned in the feeding compartment. Then the fish was released by removing the partition. Pre-experimental conditioning and isolation of the fish during prey introduction are useful practices for reducing extraneous factors that could influence the behavior of the fish.

Measurements of RD appear to be replicable within and between experiments. Werner and Hall (1974) reported standard errors equivalent to 3 to 5% of the mean in experiments with two bluegill (Lepomis macrochirus). In 9 to 28 trials with two rainbow trout (Salmo gairdneri) feeding on five size classes of prey, standard errors were less than 10% of the mean RD (Ware 1972). Confer et al. (1978) found no significant differences among lake trout (Salvelinus namaycush) of similar sizes. Among a group of eight pumpkinseed (Lepomis gibbosus), the responses of six were statistically indistinguishable (Confer and Blades 1975b). O'Brien (1979) compiled RD vs prey size data from several sources and found a good agreement between experiments.

(2) Prey selection. Reactive distance is incorporated into many mathematical models of fish predation on zooplankton (Confer and Blades 1975a; Confer et al. 1978; Eggers 1977; O'Brien et al. 1976; Ware 1973; Werner and Hall 1974). These models consistently indicate that the probability of encountering prey (a function of RD) is of primary importance in determining the diet of fish at low prey densities. At higher densities, a fish may see more than one prey at once, and the fish's diet will then depend partially on which prey is selected. This conclusion was supported by the experiments of Werner and Hall (1974). O'Brien and his co-workers have used two methods to examine prey selection by bluegill (Lepomis macrochirus). One method (O'Brien et al. 1976) was an extension of the RD experiments described above. The fish was held behind a screen while two Daphnia magna of the same or different sizes were positioned in the aquarium; the fish was then allowed to swim through an opening in the screen. The experimenters noted which prey was selected and the distances of both prey from the fish when pursuit began. They determined that bluegill select the prey with the largest apparent size, regardless of the actual size of the individuals offered. Thus, a small D. magna close to the fish might be selected over a larger individual at a greater distance. The authors determined that the data of Werner and Hall (1974) were consistent with the apparent-size-selection hypothesis.

The other method used for determining prey preference was the "tilt box" (Vinyard and O'Brien 1975). This technique was based on the following aspects of bluegill behavior: (a) bluegill will orient their dorsal surface toward light; (b) they will orient their ventral surface toward gravity; and (c) the actual position of the fish is a compromise between the light response and the gravity response, with the light response taking on greater importance when the fish sees a prey of interest. The tilt box was a 50- by 15- by 15-cm plexiglas chamber illuminated from the side by a reflector flood lamp. Water was passed through the box with a current speed of 2 to 6 cm/s, which ensured that the fish faced the appropriate direction. A 2- by 1- by 14-cm presentation chamber was located 10 cm in front of the fish. Test fish were placed in the chamber for 1 to 2 h per day for a week to familiarize them with the environment. In each experiment, a starved fish was placed in the box in dim light for 1/2 to 1 h. The light was then turned on full, and the tilt of the fish was measured against a protractor on the rear wall of the chamber. A prey was placed in the presentation chamber, and the change in tilt of the fish was measured. The change in tilt was found to be proportional to the length of the prey, ranging from about 1° for small prey to 7° for large prey. No change in tilt occurred when prey were not presented. Small bluegill (which are entirely planktivorous) responded more than large bluegill (which eat other prey besides zooplankton).

Recently, Fisher et al. (1980) used the tilt box to measure the effect of hydrazine on bluegill (Lepomis macrochirus). Artificial prey (a piece of commercial fish food glued to a microscope slide) was used instead of live zooplankton. Individual fish were placed in the box, acclimated for 5 min in the dark, and then illuminated from the side. After 1 to 6 min the tilt was measured. A screen in front of the prey was then removed and the tilt was measured again. Each fish was used in only one experiment and was exposed to the hydrazine only during the time that it was in the tilt box (10 to 15 min). Hydrazine had no effect on the tilt before the prey was exposed, but it significantly reduced the change in tilt when the screen was removed. The chemical effect in the tilt box occurred at 0.1 mg/L; the static 96-h LC_{50} for this species was determined to be 1.08 mg/L. The authors cautioned that "drawing ecological implications from this study would be inappropriate because both the prey used and lateral light sources are not natural aspects of the bluegill's habitat. Yet, as a sensitive technique to assess toxicant stress, the dorsal light response offers a new approach for behavioral bioassay studies." As the authors point out, more information on the natural predatory behavior of the bluegill is needed before the biological significance of the dorsal light response can be determined.

(3) Capture success. Planktivorous fish are very successful in capturing most prey they pursue. Pumpkinseed (Lepomis gibbosus) were 100% successful at capturing Daphnia magna and D. pulex in RD experiments (Confer and Blades 1975a), and rainbow trout (Salmo gairdneri) were 84 to 91% successful at capturing amphipods (Ware 1972). The capture success of L. gibbosus for copepods averaged 80%, with daily variances possibly due to learning by the fish. The copepods became sluggish after 36 h in the laboratory, which added to the variability in capture success (Confer and Blades 1975a). Copepods are stronger, faster swimmers than cladocerans; they are also negatively rheotactic and, therefore, swim away from the suction currents produced by planktivorous fish (Janssen 1976). Drenner et al. (1978) constructed an artificial suction device to test the avoidance capabilities of various zooplankton species. The capture frequency for Ceriodaphnia reticulata and Daphnia galeata mendotae was the same as for neutrally buoyant bubbles and heat-killed Daphnia; D. pulex escaped somewhat more successfully, and Cyclops sp., Mesocyclops sp., Diaptomus pallidus, and Chaoborus sp. avoided the suction strongly. Janssen (1976) used a similar device to demonstrate that

suction currents capture more Daphnia retrocurva than Diaptomus oregonensis. Brooks and Dodson (1965) suggested that the escape capabilities of Cyclops bicuspidatus thomasi were responsible for that species remaining in Crystal Lake, Connecticut, in the face of predation by the alewife (Alosa pseudoharengus), which had eliminated all other zooplankton of the same size. Evasion is a function of temperature; arctic grayling capture copepods more successfully at 5°C than at 15°C (O'Brien 1979). As noted by Drenner et al. (1978), the ability of zooplankton to avoid capture by fish has drawn little attention in predation studies despite the fact that this phenomenon is fairly easy to measure in the laboratory.

(4) Handling time. The interval between seizure of prey and swallowing is known as handling time. Werner (1974) measured handling times for bluegill (Lepomis macrochirus) and green sunfish (L. cyanellus) feeding on various types of prey. His method was exceedingly simple: a fish was fed prey one at a time while an observer with a stopwatch measured the time between seizure and swallowing. Handling time was relatively constant, approximately 1 s, for small prey and rose steeply for prey nearly as large as the mouth of the fish. Handling time for a given prey size increased gradually as the fish continued eating because satiated fish swallowed prey 2½ to 3 times more slowly than hungry fish. Ware (1972) observed a similar effect with rainbow trout (Salmo gairdneri), noting that partially satiated fish often rejected a prey several times before swallowing. Handling time sets an upper limit to feeding rates at high prey densities (Ware 1972) and may restrict small fish to small prey under these conditions (Werner 1974), but this is not likely to be significant in most natural situations.

(5) Population experiments. All of the experiments just described involved close observation of mechanisms involved in individual predation events. The results of these studies were used to identify critical factors in the predator-prey interaction and formed the basis for many mechanistic models of fish predation on zooplankton. To test the predictions and implications of these models and, in some cases, to derive values for model parameters, a different experimental approach has been used in which fish are allowed to feed on a zooplankton population or community rather than one individual at a time. The outcome of such an experiment is determined by comparing the surviving prey population with the initial population or by analyzing the stomach contents of the fish. The objective is to assess the feeding selectivity of the predator without necessarily distinguishing the mechanisms of selection.

The work of Drenner et al. (1978) is typical of this approach. Experiments were conducted in plastic swimming pools containing 120 to 150 L of water. Gizzard shad (Dorosoma cepedianum) were placed in the pools (31 to 38 fish per pool), and a freshly collected zooplankton community was mixed into the water. The zooplankton were sampled periodically, and experiments lasted from 1 to 13.5 h. Cladocerans

(*Daphnia galeata mendotae* and *Ceriodaphnia reticulata*) were consumed most rapidly, cyclopoids (*Cyclops* sp. and *Mesocyclops* sp.) less rapidly, and the calanoid *Diaptomus pallidus* least rapidly. These results were consistent with conclusions reached in experiments with artificial suction feeders (Drenner et al. 1978; Janssen 1976).

Werner and Hall (1974) adopted a similar approach for experiments with bluegill (*Lepomis macrochirus*). Ten fish were acclimated in pools (1.3 to 1.7 m in diameter, 15 to 28 cm deep) for 24 h, and then *Daphnia magna* were added at various densities and size class proportions. To avoid significant changes in the prey populations, the fish were allowed to feed for only 0.5 to 5 min and were then removed from the pool and their stomach contents analyzed. The results indicated that large prey were consumed in greater proportions than their proportions in the prey population. The authors analyzed the data in terms of a model based on foraging energetics. O'Brien et al. (1976) later demonstrated that the same data could be explained by an apparent-size-selection model (see above).

Zaret (1972) examined the relative preference of *Melaniris chagresi* (a tropical planktivore) for two forms of *Ceriodaphnia cornutum* by allowing two fish to feed for approximately 1 h on a mixture of the two forms and then analyzing the fish stomach contents. The feeding time was selected to permit the fish to consume 10 to 30% of the prey. As noted above, this fish was difficult to handle in the laboratory. Two to three fish were added to each 38-L aquarium the day before the experiment, and one fish had usually died by the time the experiment began. These experiments confirmed the preference of *M. chagresi* for the more visible (larger eye pigmentation area) form of *C. cornutum*.

Ware (1972) measured the consumption rate of rainbow trout (*Salmo gairdneri*) on the amphipods *Crangonyx richmondensis* and *Hyalella azteca* at different prey densities and in the presence of different litter substrates. The amphipods were placed in the 90- by 45- by 45-cm aquarium 1 h before the experiment began to allow them to disperse and find cover. One fish was then added and observed for 50 min. Attacks and captures were recorded, and the number of surviving prey was determined at the end of the feeding period.

(6) Evaluation. Predation by fish on zooplankton is an important phenomenon in aquatic ecosystems. Interference with fish-zooplankton interactions could have significant economic consequences as well since the diet of many commercial and game fish consists mainly of zooplankton or planktivorous fish. Because hundreds of laboratories throughout the country are presently equipped to culture fish and zooplankton for single-species bioassays, the incorporation of predation tests into chemical hazard assessments would not require facilities or skills not already available.

The sensitivity of fish-zooplankton interactions to toxic chemicals is unknown. Effects on the visual acuity, swimming speed, agility, and behavior of the fish would probably have a greater influence on predation than any physiological or behavioral impairment of the zooplankton. Exposing the predator, instead of (or in addition to) the prey, to a test chemical would be a logical experimental approach. Of the various parameters measurable in mechanistic studies, reactive distance is most likely to be influenced by toxicants. The reactive distance of an individual fish for a given class of prey can be measured in a few hours, but the measurement is labor-intensive and replicates would have to be run sequentially rather than simultaneously. The population approach described above is a more efficient means of measuring effects on fish-zooplankton systems since experiments can be set up with many replicates at once, and surviving prey can be preserved and counted when convenient. The studies by Drenner et al. (1978) are good examples of the population approach to fish-zooplankton interactions.

Because light intensity, turbidity, and background all have significant effects on the ability of fish to locate zooplankton, experimental conditions must be carefully controlled in fish-zooplankton studies. Hunger and feeding experience of the fish are critical in any predation experiment. The age and size of both predators and prey must be specified, and other factors (configuration of the test chamber, timing of the experiments, and potential interference by the observer) can also influence the results. All these variables should be rigidly standardized among tests and among laboratories if consistent results are to be achieved.

The ecological and economic significance of fish predation on zooplankton and the widespread familiarity with these animals as subjects of bioassays justify incorporation of fish-zooplankton predation tests in the battery of hazard assessment methods. Studies should be undertaken to determine the sensitivity of fish-zooplankton interactions to toxic chemicals and to optimize the experimental procedure for routine testing.

3.2.4 Fish-Macroinvertebrates

A survey of the literature indicated that little laboratory research has been done on predation by fish upon macroinvertebrates. Two groups of studies are reviewed here: (1) a series of experiments on predation by estuarine fish on grass shrimp conducted at EPA's Gulf Breeze Environmental Research Laboratory (ERL) and (2) a group of studies concerning the interactions between smallmouth bass and crayfish. Grass shrimp and crayfish, both detritivores, are important components of the food webs of coastal ecosystems and lakes, respectively.

(1) Predation on grass shrimp. Tagatz (1976) reported the first of a series of predation experiments involving the grass shrimp,

Palaemonetes pugio. His experiments were performed in model ecosystems similar in concept to the terrestrial-freshwater microcosms of Metcalf et al. (1971). The model ecosystems consisted of 4 cm of sand and 160 L of artificial seawater in 180-L aquaria. Turtle grass (*Thalassia testudinum*) was planted over two-fifths of the bottom surface, and 75 grass shrimp were added. The systems were allowed to equilibrate for 4 to 6 days, and mirex was then added. There was no significant mortality of shrimp for 13 days in these systems compared to controls. After 13 days, two pinfish (*Lagodon rhomboides*) were introduced into each tank, and the numbers of surviving shrimp were determined after 1 to 3 days of predation. Predation was significantly higher in systems treated with mirex than in the controls. The author recognized that the results might have reflected effects of mirex on either the predator or the prey, but concluded on the basis of previous toxicity tests that only shrimp were affected. He stated that the concentration of mirex found to alter the predator-prey interaction (0.025 µg/L) was "the lowest concentration of mirex in water that has been reported to cause death of an estuarine animal." Death in this case was an indirect result of exposure to the toxicant.

Tagatz (1976) believed that the effects of mirex were caused by alterations in the behavior of the grass shrimp, but he reported no observations that would support this contention. Farr (1977) conducted experiments specifically designed to reveal behavioral alterations in shrimp exposed to toxicants. He conditioned Gulf killifish (*Fundulus grandis*) to feed on grass shrimp introduced into the aquarium with a dip net. Ten shrimp were presented to each fish daily, and the survivors were removed after a 3-h feeding period. When the fish had become accustomed to this procedure, Farr exposed groups of shrimp to methyl or ethyl parathion for 24 to 72 h and then fed them to the killifish as usual. He measured the time between the consumption of the first shrimp and the capture of the third and counted the survivors after 15 min and again after 3 h, when the remaining shrimp were removed. A single run consisted of one fish, which was fed control shrimp one day and treated shrimp the next; thus, each run included its own control. Farr found that parathion significantly reduced the time needed for the fish to capture the second and third shrimp and increased the number of shrimp consumed in 15 min. There were no effects on the total number of shrimp captured in 3 h (probably because there were few survivors even among controls). Treated shrimp were more active than controls and therefore presumably more conspicuous to the fish. Since parathion also decreased their physical endurance, the shrimp were easier for the fish to catch.

In a subsequent study, Farr (1978) examined prey selection by killifish which were offered grass shrimp and sheepshead minnows (*Cyprinodon variegatus*) simultaneously. Equal numbers of shrimp and minnows were placed in aquaria, and some were exposed to methyl parathion for 24 h. One killifish was then added to each tank, and prey survival was monitored for 5 days. In tanks without parathion, minnows were consumed more rapidly than shrimp. Parathion caused increased predation on both species, but shrimp were affected more strongly than minnows, and selection by the predator was apparently reversed for a time. This effect was more pronounced at higher parathion concentrations. Farr presented the results in three ways: (a) as percent survival of each species; (b) as the ratio of surviving shrimp to surviving minnows; and (c) as a capture coefficient equal to the ratio of prey species consumed, divided by the ratio of prey species available to the predator. Presentations (b) and (c) both indicated that parathion erased the predator's preference for minnows, but only (a) revealed that the survival of treated minnows averaged 61% of controls. Farr did not mention this latter result and omitted statistical treatment of the data in (a); therefore, the significance of the effect on minnows is unknown. The two-prey system (Farr 1978) may be an improvement over the one-prey experiments (Farr 1977), but inconsistencies in the 1978 paper make an objective evaluation impossible.

Experiments on predation on grass shrimp continued for a time after Farr's departure from the Gulf Breeze ERL, but have now been suspended; further research has been directed towards single-species behavioral bioassays (C. R. Cripe, personal communication).

(2) Predation on crayfish. Factors affecting predation on crayfish (*Orconectes propinquus*) by smallmouth bass (*Micropterus dolomieui*) were investigated by Stein and Magnuson (1976) and by Stein (1977). Experiments were conducted in flow-through aquaria with sand, pebble, or gravel substrates. In a typical experiment, equal numbers of four size classes of crayfish were placed in tanks with one bass; surviving crayfish were removed, counted, and returned to the tanks every 2 h (Stein 1977). (In other experiments, survivors were counted daily.) Variations on this experimental design were used to measure predation as a function of the sex, reproductive condition, and molting stage of the crayfish (Stein 1977) and as a function of substrate type (Stein and Magnuson 1976). These experiments lasted from 10 h to 7 days.

The handling time for bass feeding on crayfish was measured in another series of experiments (Stein 1977). An opaque tube was placed vertically in the water, and a crayfish was added. When the crayfish settled to the bottom of the tube, the tube was removed; the bass were trained to eat crayfish presented in this way. The time from capture to swallowing (the handling time) was measured in each encounter. Handling time varied with prey size and molting stage. Using an approach similar to that of Werner and Hall (1974) [Sect. 3.2.3(5)], Stein used the data to predict the prey size that would optimize the predation efficiency of the bass (pursuit plus handling time divided by energy gain).

The presence of a predator was found to influence the behavior of crayfish (Stein and Magnuson 1976). Various activity patterns wer quantified for 3 days without fish. Bass were then introduced into some aquaria, and crayfish behavior was monitored for 3 more days. In the presence of the predator, active behavior patterns (such as walking, climbing, grooming, and feeding) were reduced, and the crayfish spent more time hiding in the substrate. Crayfish in tanks with bass also preferred pebble to sand because the former substrate offered greater opportunity for hiding; this preference was not seen when no fish were added. In all cases, behavioral effects were most noticeable among prey groups most susceptible to predation (juveniles and nonreproductive adults).

(3) Evaluation. The evaluation of fish-macroinvertebrate tests as hazard assessment tools is included with the evaluation of fish-fish systems in Sect. 3.2.5(3).

3.2.5 Fish-Fish

Predator-prey interactions among fish have been the subject of numerous laboratory investigations during the past 10 years. Most experiments have been designed to compare the vulnerability of two or more groups of prey. The groups may be different species (Coble 1973; Herting and Witt 1967; Mauck and Coble 1971) or members of the same species differing in size, color, form (Coble 1973; Mauck and Coble 1971), physiological condition (Coble 1970; Herting and Witt 1967; Vaughan 1979), or previous exposure to chemical or physical stress (Baker and Modde 1977; Coutant 1973; Coutant et al. 1974; Deacutis 1978; Goodyear 1972; Kania and O'Hara 1974; Sullivan et al. 1978; Sylvester 1972, 1973; Woltering et al. 1978; Wolters and Countant 1976; Yocum and Edsall 1974). Examples of recent research and a discussion of methodological details are presented in this section.

(1) Examples of recent research. The focus of many predator-prey studies with fish has been the effects of toxicants or thermal stress on the susceptibility of prey to predation. Kania and O'Hara (1974) exposed groups of mosquito fish (*Gambusia affinis*) to 0.005 to 0.1 mg/L of mercury and offered each group, along with equal numbers of untreated mosquito fish, to largemouth bass (*Micropterus salmoides*). After 60 h, all the remaining mosquito fish were collected and counted. It was found that short exposure to low levels of mercury impaired the normal escape behavior of the prey, and predation was heavier on the treated group than on the controls. The effect was a function of mercury concentration and was seen as low as 0.01 mg/L, which is well below the lethal concentration for this fish.

Woltering et al. (1978) studied the effects of ammonia on the interaction between largemouth bass and mosquito fish. The approach differed from that of Kania and O'Hara (1974); predator and prey were both exposed to the toxicant continuously throughout the experiment. Ammonia concentrations above 0.34 mg/L caused physiological and behavioral changes in the predator, resulting in a lowered predation rate. The effect was greatest at high prey densities, where the predator was actively harassed by the prey. Like Kania and O'Hara (1974), Woltering et al. (1978) observed changes in the predator-prey interaction at toxicant concentrations below the lethal level.

The effects of acute and chronic exposure to cadmium on the vulnerability of fathead minnow (*Pimephales promelas*) to predation by largemouth bass were examined by Sullivan et al. (1978). Subtle behavioral changes in the prey increased their vulnerability at cadmium concentrations less than one-hundredth of the reported maximum allowable toxicant concentration (MATC) for this species. These changes are described in detail by Sullivan and Atchison (1978).

Increased predation on thermally stressed fish was reported in a series of papers by Coutant and co-workers (Coutant 1973; Coutant et al. 1974; Coutant et al. 1979; Wolters and Coutant 1976). In one study (Coutant 1973), juvenile rainbow trout (*Salmo gairdneri*) and chinook salmon (*Oncorhynchus tshawytscha*) were exposed to elevated temperatures for varying lengths of time and then placed in a tank with adult rainbow trout. When about 50% of the prey had been consumed, the survivors were removed and counted. The stressed fish exhibited disorientation, erratic swimming, unnatural posture, and reduced escape abilities; consequently, they suffered higher predation than unstressed prey. The effects were related to the exposure temperature and exposure time and were significant at 11% of the median lethal time or 2.5°C below the median lethal temperature. The experiments were intended to simulate the actual experience of juvenile fish near the thermal discharge of the Hanford, Washington, nuclear reactor.

In a subsequent study, Coutant et al. (1974) acclimated juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass to several above-normal temperatures and then placed them with adult largemouth bass at 16°C. When the acclimation temperature was 7 to 9°C higher than the predation temperature, the prey were "benumbed" and rested on the bottom rather than seeking refuge. The predators recognized and preferentially selected the shocked fish. A much greater thermal shock is necessary to kill these fish. Wolters and Coutant (1976) observed similar effects with cold-shocked bluegill (*Lepomis macrochirus*). Other studies on thermal effects include those by Deacutis (1978) with killifish (*Fundulus majalis*) feeding on larvae of Atlantic silverside (*Menidia menidia*) and flounder (*Paralichthys dentatus*); by Sylvester (1972, 1973) with coho salmon (*Oncorhynchus kisutch*) feeding on sockeye salmon fry (*O. nerka*); and by Yocum and Edsall (1974) with yellow perch (*Perca flavescens*) feeding on fry of lake whitefish (*Coregonus clupeaformis*).

Goodyear (1972) demonstrated increased predation by largemouth bass on mosquito fish that had been exposed to gamma radiation. In this experiment, the prey were provided with refuge from the predator, and nonirradiated fish could survive for 20 days with only 5% losses. However, irradiated fish tended to wander out of the refuge, and 60% were consumed in 20 days. Goodyear proposed the method as a simple screening test for toxicants.

Several investigators (Coble 1970; Herting and Witt 1967; Vaughan 1979) have studied the influence of disease, parasitism, and viral infection on the predator-prey interaction. Herting and Witt (1967) presented bowfin (*Amia calva*) with pairs of prey species including golden shiner (*Notegonus chrysoleucas*), bluegill, green sunfish (*Lepomis cyanellus*), and largemouth bass. The preference of bowfin for one prey species over the other could be reversed if one of the prey species was diseased, parasitized, or suffered from handling stress. For example, normal bluegill were less vulnerable than green sunfish when both were offered together to the predator, but bluegill suffering from columaris disease were more vulnerable than green sunfish. A similar reversal was seen when largemouth bass parasitized by trematodes were offered together with healthy golden shiners. The authors concluded that the changes in relative vulnerability were due to sluggish behavior, which drew the attention of the predator (bowfin prefer slow-moving or stationary prey) and reduced agility and stamina of the prey. Vaughan (1979) as well as Coble (1970) observed no increased vulnerability in bluegill infected with lymphocystis virus or in fathead minnows infected with yellow grub (*Clinostomum marginatum*) respectively. Vaughan (1979) suggested that these negative results were due to the absence of noticeable behavioral changes in the infected prey.

(2) *Methodological details*. Most experiments on fish predator-prey interactions have been conducted in flow-through aquaria containing 100 to 750 L of water or in pools holding up to 3600 L of water. Deacutis (1978) studied predation by small killifish in 9-L tubs; at the other end of the size range, Mauck and Coble (1971) performed experiments in 0.04-ha ponds. Ginetz and Larkin (1975) constructed experimental troughs in a salmon spawning channel for studies of rainbow trout feeding on sockeye salmon fry. Most workers, however, have used conventional fish tanks.

In many cases, cover or refuge was provided for prey and/or predators. Cover has consisted of artificial vegetation (Coble 1973; Sullivan et al. 1978; Vaughan 1979), tree limbs (Mauck and Coble 1971), or bricks (Coble 1973). In Goodyear's (1972) studies of largemouth bass predation on mosquito fish, a shallow refuge area was provided for the prey, separated from the main portion of the aquarium by a coarse screen. The screen was necessary because some bass would pursue the prey into the shallow area, whereas others would not, creating variability in the experimental results. Shallow refuge areas were used by Kania and O'Hara (1974) and Woltering et al. (1978) in experiments with the same two species. Provision of refuge or cover for the prey increases their chances of survival and creates a more realistic environment for the predator-prey interaction. When no cover is present, the prey are usually consumed within minutes. Wolters and Coutant (1976) did not provide cover and reported difficulty in terminating some of their experiments before 50% of the prey were consumed since this sometimes occurred in less than 1 min. With cover, and especially with a refuge, experiments can be continued for several weeks if desired (Goodyear 1972).

Experiments have been conducted using fish from laboratory stocks as well as fish from the field. In either case, the fish must be preconditioned to the experimental situation. Acclimation to a particular temperature or light intensity can affect the performance of predator and prey (Coutant et al. 1974; Ginetz and Larkin 1976; Sylvester 1972; Wolters and Coutant 1976; Yocum and Edsall 1974). Learned behavior on the part of both animals also plays an important role in predation studies and can be a source of unexpected variability in the results. For instance, Baker and Modde (1977) reported that bluegills were timid in their first two encounters with blacktail shiners (Notropis venustus), but beginning with the third trial, they became more aggressive and actively searched for prey. Most investigators have trained the predators to feed under experimental conditions; Goodyear (1972) and Woltering et al. (1978) conditioned the prey to the predator as well.

In comparisons of predation on different groups of prey, the different groups may be offered to the predator simultaneously or in separate trials. When more than one prey type is present in one aquarium, differential marking is sometimes necessary to distinguish the groups. Many workers (e.g., Coutant 1973; Sullivan et al. 1978) used cold branding to identify treated and control prey. Kania and O'Hara (1974) used a radioisotope (^{197}Hg) to tag mosquito fish exposed to mercury; FitzGerald and Keenleyside (1978) suggested ^{131}I for the same purpose. Some marking techniques may affect the vulnerability of the prey. For example, Baker and Modde (1977) demonstrated that blacktail shiners marked with a particular stain were selected by largemouth bass and bluegill over unmarked shiners. Fin clipping is another marking technique that can affect the predator-prey interaction (Mauck and Coble 1971).

When alternative prey are presented to the predator simultaneously, the ratio of prey abundances can influence selection by the predator (Coutant 1973; Coutant et al. 1979). Results of an experiment may then depend on the proportions of prey added initially and on changes in those proportions during the test. To minimize this factor, experiments are often terminated before half of the prey are consumed (Coutant 1973; Coutant et al. 1974; Mauck and Coble 1971; Vaughan 1979; Wolters and Coutant 1976).

When different groups of prey are presented to the predator in separate trials, the problems of differential marking and prey proportions are avoided, but identical conditions must be carefully maintained from one trial to the next. The size, experience, and physiological condition of the animals are important factors in predation experiments. Predators are usually starved for 24 h or more before each experiment to achieve a uniform degree of hunger. Yocum and Edsall (1974) exposed the same predators to stressed and nonstressed prey alternately, with each group of predators serving as its own control. (A similar approach is often used in studies of fish predation on zooplankton--see Sect. 3.2.3).

In a few instances, predators and prey have been exposed to stress together in the same experimental chamber instead of exposing the prey separately and then adding them to the tank. The studies of Tagatz (1976) and Farr (1978) are discussed in Sect. 3.2.4(1), and those of Woltering et al. (1978) are described above. We found no reports of experiments in which only predators were exposed to a toxicant or other stress.

The outcome of a fish predator-prey experiment is usually determined by counting the surviving prey. When different prey groups are presented to predators in separate trials, analysis of variance is used to test for treatment effects (e.g., Ginetz and Larkin 1976; Sylvester 1973). When different prey groups are presented simultaneously, the results are often expressed as some type of selection index (e.g., Baker and Modde 1977; Coutant 1973; Coutant et al. 1974; Herting and Witt 1967; Mauck and Coble 1971; Wolters and Coutant 1976). Alternatively, a chi-square test may be used to compare the proportions of prey consumed with the proportions initially present (e.g., Coble 1973; Kania and O'Hara 1974). Sullivan et al. (1978) developed a special statistical technique for analyzing predation results.

A few investigators have measured the results of predator-prey experiments in ways other than counting survivors. Yocum and Edsall (1974) and Deacutis (1978) counted the number of attacks, captures, and escapes during experiments. This approach made it possible to differentiate effects on prey attractiveness (as indicated by frequency of attacks) from effects on escape abilities (as indicated by the ratio of captures or escapes to attacks). In both these studies, heat-stressed prey were attacked less frequently, but captured more successfully, than controls. Sylvester (1972) recorded the time of capture of each prey and expressed the results as the mean survival time of the prey. Yocum and Edsall (1974) found this approach unsatisfactory with yellow perch feeding on whitefish fry because individual predators differed greatly in the time taken to discover the prey. Woltering et al. (1978) measured the growth of predators during 10-day experiments; the results reflected the same trends as numbers of prey consumed.

(3) Evaluation. The studies of Tagatz (1976) and Farr (1977 1978) on predation by fish on grass shrimp are well-known examples of chemically induced alterations in prey behavior leading to increased susceptibility to predation. The predator's role in these

experimental systems is to detect the behavioral alterations. If a human observer were equally perceptive, the tests could be simplified to single-species behavioral bioassays. The same is true of most of the fish-fish studies discussed in this section. As stated above, the major justification for employing this type of predator-prey system in hazard assessment is its extreme sensitivity to chemical stress.

In most other respects, what has been said in Sect. 3.2.3(6) about fish-zooplankton interactions applies here as well. Fish-shrimp and fish-fish systems are somewhat more complex than fish-zooplankton systems, since a refuge or cover should be provided for the prey to permit ecologically significant behavioral effects to be revealed. Another difference between these experiments and those with zooplankton is that shrimp or fish prey may have equal or greater economic importance than the predator.

There are no serious obstacles to the development and standardization of predator-prey test procedures with shrimp or fish as prey. A predation experiment could be a convenient sequel to a single-species acute bioassay. For example, shrimp could be exposed to a range of chemical concentrations for determination of an acute LC_{50}. The animals from the sublethal treatments could then be presented to a predator to determine whether their survival abilities had been impaired. An integrated testing sequence such as this would provide a more ecologically meaningful indication of the potential hazards of a chemical than conventional bioassays alone, with no serious increase in cost.

3.2.6 Conclusions and Recommendations

All the predator-prey interactions discussed, except for protozoan predation, are of known ecological significance. Many have been shown to be highly sensitive to chemicals and other types of disturbance. Tests for chemical effects on the interaction between any two species are not likely to provide reliable information about interactions between other species pairs or to permit accurate predictions of effects that would occur in the context of a whole community or ecosystem. Therefore, the most suitable position for predator-prey tests in a chemical hazard assessment sequence is immediately after screening tests.

Laboratory systems with zooplankton predators and prey are probably the most efficient for chemical testing. Many zooplankton species are easily cultured, and large reproductive populations can be maintained in static aquaria. Predation tests can be conducted in small, static systems. Experiments can be completed in 8 h or less, and the surviving prey can be preserved to be enumerated later. Because zooplankton are nonvisual predators, lighting is not a critical factor, and experiments can be conducted in darkness. Learning, social interactions, and disturbances caused by observers are much less important in zooplankton-zooplankton systems than in fish systems. The most likely mechanisms for chemical effects on zooplankton predation are: (1) reduced swimming speed of predators or prey, (2) reduced capture success of predators, or (3) reduced escape success of prey. The sensitivity of these mechanisms to chemicals is unknown. Replicability of zooplankton-zooplankton systems is probably good. Species that might be suitable predators in chemical test systems include *Mesocyclops edax* and *Cyclops* spp., while *Diaptomus* spp., *Bosmina longirostris*, and *Ceriodaphnia* spp. would be appropriate prey.

Fish-zooplankton predation tests are somewhat more complicated than tests with zooplankton predators. Fish cultures require more space than zooplankton cultures, and continuous flow systems are necessary for most species. Likewise, predation studies involving fish generally require large volumes and/or continuous flow. Lighting conditions and background must be carefully controlled to ensure repeatable results with these visual predators. Effects of learning, social behavior, and unintentional disturbances are more likely to occur with fish than with zooplankton predators. All these factors imply that fish-zooplankton systems would be less amenable to chemical hazard assessment than zooplankton-zooplankton systems. However, experiments with fish might be faster than zooplankton predation tests since fish consume more prey in a given time than do zooplankton.

Possible mechanisms for chemical effects on fish-zooplankton interactions include: (1) impaired vision of the fish; (2) reduced swimming speed of predator or prey; and (3) reduced avoidance ability of prey. The sensitivity of fish-zooplankton systems to chemicals is unknown, but might be enhanced if zooplankton with well-developed escape abilities (such as *Diaptomus* spp.) were used as the prey. Replicability may be a problem with these systems because so many experimental variables can affect the results.

Because of the social and economic importance of many planktivorous fish, an attempt should be made to develop an efficient fish-zooplankton test system. The problems discussed above indicate that test procedures would have to be specified in considerable detail, but the problems are not insurmountable in developing a protocol. Common bioassay organisms such as rainbow trout, bluegill, and *Daphnia* could be readily applied to predator-prey experiments.

Predation experiments with fish as predators and macroinvertebrates or fish as prey have the same technical complications as fish-zooplankton experiments, but to a greater degree. Nevertheless, relatively simple fish-fish systems have been successfully used to test for effects of stress. The sensitivity of fish-shrimp and fish-fish systems to chemicals has been demonstrated; indeed, these are the only predator-prey systems for which we have information on chemical effects. The largemouth bass-mosquito fish systems of Goodyear (1972), Kania and O'Hara (1974), and Woltering et al. (1978) have proved quite amenable to effects testing, as have many other systems described in Sects. 3.2.4 and 3.2.5. The background of experience with chemical effects tests in such systems may offset the inherent difficulty of devising suitable test protocols. It is recommended, therefore, that a tentative protocol be developed for fish-fish (or fish-shrimp) experiments and that they be compared with zooplankton-zooplankton and fish-zooplankton systems before a final decision is reached on the best system for hazard assessment. It is also recommended that research be conducted to devise sensitive, objective indicators of subtle behavioral effects, with the ultimate objective of replacing fish-fish and fish-shrimp tests with simple, single-species behavioral assays since alteration of prey behavior is the most likely mechanism of chemical effect on these interactions.

To summarize the recommendations in this section, tests with fish as predators and either fish or shrimp as prey are well-known and could be standardized for chemical hazard assessment in the near future. Tests with zooplankton as predators or prey are potentially easier to use than fish predation tests, but further research must be conducted before zooplankton-zooplankton or fish-zooplankton systems can be adapted to chemical testing. Protozoa-protozoa predation tests are not recommended for development in this context.

3.3 Parasitism

It is widely recognized that the incidence of parasitism or disease in a population is determined partially by the physiological state of the host organism and that various environmental stressing agents can reduce the host's resistance to infection (Snieszko 1974; Wedemeyer 1970). Snieszko (1974) cited several instances of increases in parasitic infections in fish exposed to pesticides. Draggan (1977) reported indirect evidence of effects of chromium on the interaction between carp eggs and a fungal parasite. However, these observations were incidental to studies conducted for other purposes. Effects of drugs on parasitism and disease are, of course, the subject of clinical parasitology, which is outside the scope of this review.

The only example found of an experiment specifically designed to measure chemically induced susceptibility to parasitism was that of Couch and Courtney (1977). These authors examined penaeid shrimp from the Gulf of Mexico and found a high incidence of *Baculovirus* infection in the population. Infected shrimp were identified by microscopic examination of hepatopancreatic cell nuclei. A group of 925 shrimp was exposed to 0.7 μg/L Aroclor® (a polychlorinated biphenyl) for 35 days, and the incidence of parasitic infection in the population was compared with a control group held under similar conditions. Infected shrimp initially comprised 23.3% of the population. After 35 days, 45.7% of the control group were parasitized, compared with 75% of the shrimp exposed to PCB. Mortality was 13% in controls and 50% in treated shrimp. It was impossible to separate direct PCB toxicity from mortality resulting from increased parasitism without a parallel experiment using noninfected animals. The authors recognized the need for such an experimental design, but found it to be impossible due to an inability to raise shrimp xenobiotically and to detect latent viral infections in apparently healthy shrimp. Possible mechanisms for the observed effects of PCB on this host-parasite system were: (1) loss of resistance of shrimp to new viral infections; (2) enhancement of latent infections; (3) increased virulence of the virus; or (4) increased cannibalism on intoxicated individuals (cannibalism being one mechanism by which the virus is transmitted through the population). PCB was found to accumulate in the site of infection (the hepatopancreas), but not in tail muscle, which was uninfected.

The large numbers of animals involved in this study and the number of histopathological examinations required to determine the effect of one chemical at one concentration in one treatment group lead to questions about the practicality of this system for routine chemical hazard assessment. An earlier attempt to demonstrate the same effect using fewer individuals and shorter exposure times was inconclusive (Couch 1976). Moreover, the effect of PCB on the shrimp-Baculovirus system is probably not generalizable to any other host-parasite interaction. A chemical that failed to produce an effect in the shrimp-Baculovirus test would not necessarily be innocuous in other situations. We conclude that there are no host-parasite systems amenable to development as hazard assessment tests at this time. It is recommended that the parasitological literature be surveyed to evaluate the possiblity of developing a hazard assessment protocol.

3.4 Plant-Herbivore Interactions

The major plant communities in aquatic ecosystems are phytoplankton and macrophytes. Grazing on macrophytes has been studied very little by ecologists, and no relevant laboratory studies were found in our review of the literature. Grazing by zooplankton on phytoplankton is recognized as an important component of ecosystem energy flow and nutrient cycling and as a possible determinant of plankton community structure, but it too has received little attention. One reason for this is that methods for measuring plankton grazing rates, either in situ or in the laboratory, are still poorly developed. The sensitivity of zooplankton grazing to chemical stress is not known and should be investigated.

A phytoplankton-zooplankton hazard assessment test would be essentially a single-species bioassay, with zooplankton grazing rate as the measured response. Inert particles could be (and often are) substituted for algae in this type of test without changing the nature of the experiment significantly. The literature was not searched thoroughly for laboratory phytoplankton-zooplankton systems because our attention was directed towards areas with more promise for chemical hazard assessment.

It should be noted that grazing is one of the important processes in mixed flask culture model ecosystems [Sect. 3.6.3(1)]. It is, however, difficult to separate grazing from other processes occurring simultaneously in these systems.

3.5 Symbiosis

No published reports of chemical effects on symbiotic interactions among aquatic organisms were found. Because symbiosis represents a high degree of specialization on the part of the interacting species, chemical effects on one species pair would probably not be relevant to other pairs. With the possible exception of zooxanthellae in coral polyps, symbiosis is less important in aquatic ecosystems than any of the other interactions reviewed in this report. Symbiosis does not seem to be a logical subject for inclusion in a chemical hazard assessment program.

3.6 Ecosystem Properties

All organisms in nature live in ecosystems. The structural and functional properties of ecosystems determine the context in which organisms, populations, and communities develop, persist, and interact. Therefore, chemical effects on ecosystem properties have the potential to influence all the components of the ecosystem. In some situations, effects on ecosystem properties may be direct consequences of easily observed effects on dominant organisms, and knowledge of the responses of those organisms may be sufficient to infer hazards to ecosystems. In other instances, the mechanisms of ecosystem effects may be obscure. In either case, the ramifications of ecosystem-level effects on all components of an ecosystem can be unpredictable and far-reaching. This is the major justification for the development of methods to assess the hazards of chemicals to ecosystems.

This section reviews the properties of aquatic ecosystems and discusses the central issue of laboratory studies at the ecosystem level--the problem of predicting effects on natural ecosystems from responses measured in simplified laboratory systems. Finally, some general types of laboratory model ecosystems, or microcosms, that might be adaptable for chemical hazard assessment under TSCA are described.

3.6.1 Properties of Aquatic Ecosystems

An ecosystem is essentially an energy processing unit. Incoming solar energy is converted first to chemical energy and finally to heat. Because the energy processing capacity of an ecosystem depends on a steady supply of inorganic nutrients, the ecosystem expends a certain fraction of the energy it processes to ensure that nutrients are retained and recycled. Cycling of essential elements is accomplished through interactions among components of the ecosystem.

These interactions confer a degree of homeostatic control, which permits the maintenance of maximum persistent biomass in the face of environmental fluctuations (Whittaker and Woodwell 1972; Reichle et al. 1975). The existence of ecosystem homeostasis is implied by the persistence of complex natural systems through time. Elucidation of homeostatic mechanisms is a primary objective of ecosystem analysis.

Ecosystem function may be conceived in terms of superimposed flows of energy and matter. Conversion of solar energy in photosynthesis is accompanied by production of organic matter from inorganic elements. Chemical energy is released as heat by respiration, and the elements in organic matter are returned to inorganic form. In a mature ecosystem, the two portions of the matter-energy conversion are approximately in balance, at least over an annual cycle.

Thus, ecosystem metabolism consists of two basic processes, an anabolic or productive process and a catabolic or regenerative process. The productive process is mediated almost entirely by green plants; the rate of this process is termed gross primary productivity (GPP). The regenerative process is a function of both autotrophs and heterotrophs and represents the total energetic cost of operating the ecosystem. The difference between GPP and total ecosystem respiration (R_E) is the net ecosystem productivity (NEP), which represents storage of energy in biomass or detritus (Reichle et al. 1975). The ratio of GPP to R_E, usually referred to as P/R, is one index of ecosystem metabolism that has been measured in several aquatic ecosystems. Odum (1956) proposed the use of P/R for classifying ecosystems as autotrophic ($P/R > 1$) or heterotrophic ($P/R < 1$) and noted that either type of system tends to approach $P/R = 1$ over time. Odum (1969) listed $P/R = 1$ as an attribute of mature ecosystems, concluding that P/R could be used as an index of relative maturity. P/R ratios approximating 1 have been found in many laboratory microcosms (Beyers 1962, 1963; Copeland 1965; Gorden et al. 1969; Giddings and Eddlemon 1978; Harris et al. 1980) and natural systems (Riley 1956; Odum 1957; Odum and Hoskin 1958; Jordan and Likens 1975).

Microcosm studies consistently demonstrate that P/R departs from 1 when a system is disturbed. Microcosms grown at 23°C had a P/R of 1.09 at that temperature. When the temperature was lowered to 13°C, P/R rose to 1.27; and at 33°C, P/R was 0.81 (Beyers 1962). Microcosms dominated by turtle grass growing at 1500 foot candles (fc) had a P/R approximating 1. When the light was reduced to 230 fc, both P and R declined immediately, and P/R fell below 1. After 90 days, P and R had returned to their initial level; P/R was about 1; and the turtle grass community had been replaced by blue-green algae (Copeland 1965). Increased grazing pressure has the same effect as decreased light intensity: a decrease in both P and R, with P/R falling below 1 (McConnell 1962; Beyers 1963). In pond microcosms, P/R fell from 1.0 to 1.4 at steady state to 0 or below (i.e., negative net production) when arsenic was added and returned to 1.0 after 3 weeks (Giddings and Eddlemon 1978). Various toxic substances added to large experimental pools produced the same result (Whitworth and Lane 1969). Thus, P/R appears to be a reliable indicator of stress-induced changes in ecosystem metabolism.

Nutrient cycling is more difficult to measure than ecosystem metabolism. The easiest and most common approach to monitoring nutrient conditions in aquatic ecosystems is to measure the concentrations of dissolved inorganic nutrients. The extremely low concentrations of dissolved inorganic phosphorus and nitrogen in most lakes and ponds are evidence of the close coupling between rates of supply and rates of uptake by aquatic plants. Because of this coupling, changes in nutrient regimes may not be reflected in ambient nutrient concentrations (Schindler et al. 1971). Nutrient concentrations in sediment interstitial water may be more sensitive indicators of altered nutrient cycling than open-water nutrient concentrations (Harris et al. 1980). In a system with well-defined boundaries, the balance between nutrient inputs and outputs is a measure of the ability of the system to retain nutrients; retention of nutrients is a characteristic of mature, undisturbed ecosystems (Likens et al. 1977; Odum 1969).

Aquatic autotrophs, especially phytoplankton, respond rapidly to changes in nutrient regimes. The physiological state of autotrophs is very dependent on their nutrient status. The nutrient status of autotrophs can be assessed by measuring their response to nutrient enrichment, by determining nutrient concentrations in plant tissues, or by means of various physiological indicators such as alkaline phosphatase activity and enhancement of dark CO_2 fixation by ammonium.

Techniques exist for measurement of specific microbial processes contributing to the cycling of nutrients, including nitrogen fixation, nitrification, denitrification, sulfate reduction, and methanogenesis. Other components of the nutrient cycle, such as uptake by plants and regeneration from detritus, can be measured by isolating these processes from competing processes. However, determination of nutrient flux in whole ecosystems generally requires isotopic tracers such as ^{32}P and ^{15}N.

Very little is known about the sensitivity of nutrient cycling to toxic chemicals in aquatic ecosystems. It is possible that the structural and functional redundancy of most ecosystems would compensate for chemical effects on individual components of the nutrient cycle. Indeed, such stabilizing redundancy is one aspect of the homeostatic character of mature ecosystems. However, if a chemical were to disrupt nutrient cycling significantly, the effects on the ecosystem would be serious and unpredictable.

Techniques for measuring or predicting effects of chemicals on aquatic ecosystem properties are in an early developmental stage.

There is very little information by which to compare the sensitivity of ecosystem properties to chemicals with the sensitivity of conventional bioassay organisms. Neither do we know the degree to which responses of one ecosystem are likely to occur in other ecosystems. Research is needed on the whole gamut of potential ecosystem-level effects in a variety of ecosystems so that general answers to these questions may begin to emerge. Such research must be supported by conceptual advances in ecosystem analysis and by the development of practical techniques for measuring ecosystem properties. Thus, the search for tools for hazard assessment at the ecosystem level is inseparable from basic research into the ecology of whole ecosystems.

3.6.2 Realism and Generality

In discussing the applications of model ecosystems to chemical hazard evaluation, a distinction is often made between "generic" systems, which exhibit properties common to all ecosystems without mimicking any natural ecosystem in particular, and systems that simulate some specific ecosystem in greater or lesser detail. Such a distinction is necessary because two of the criteria for an ecosystem-level test protocol are not wholly compatible--namely, the requirements of realism and generality. Realistic simulation of any single ecosystem is achieved at the expense of generality; yet a test cannot provide information relevant to a range of ecosystem types without sacrificing some ability to represent a particular ecosystem in detail. These conflicting demands are frequently lumped together and termed "extrapolation," which refers to the general problem of using laboratory experiments to make inferences about natural phenomena. Such lumping of concepts is dangerous. The confusion arising from misunderstanding the dual nature of extrapolation has fueled much controversy about the utility and role of model ecosystems in hazard assessment.

Realistic simulation of some ecosystems is inherently more difficult than others. In terrestrial ecosystems, the size of the dominant vegetation may be the critical factor limiting the degree of simulation possible in the laboratory. In contrast, aquatic model ecosystems are constrained mainly by the dimensions of the dominant physical processes (mixing, turbulence, flow). The physical features of ponds, for example, are much easier to incorporate into laboratory systems than those of rivers, streams, or pelagic environments. Years of experience with one type of aquatic microcosm may lead investigators to make sweeping statements about the degree of realism that microcosms can achieve without appreciating that realism is a function of the ecosystem being modeled.

Likewise, some aspects of aquatic ecosystems are more readily reproduced in the laboratory than others. Realistic simulation of higher trophic levels is typically not possible in small laboratory systems. However, decomposer communities can be easily incorporated into model ecosystems. A major goal of research with any type of model ecosystem should be to identify those aspects of the system that most accurately represent the natural prototype.

It is important here to distinguish between structural and functional similarity. Exact duplication of the absolute abundances of all species is not necessary for reasonable simulation of the important processes occurring in an ecosystem. Unless a particular species has some economic, social, or aesthetic importance, its abundance may be of little concern to us. We are more concerned with the continued well-being of the system as a whole than with its structural details. Because of the functional redundancy of most ecosystems, some species can be entirely replaced by others without altering the overall productivity or persistence of the ecosystem. Conversely, research with gnotobiotic microcosms has shown that assemblages of the same species can be quite different in their functional characteristics. This is not to deny the value of good simulation of ecosystem structure in a laboratory system, but rather to emphasize that species abundance is not the only, or the best, measure of the success of simulation.

These thoughts lead quite naturally to a consideration of the other criterion for a hazard assessment tool--namely, generality. If a model ecosystem and a natural ecosystem may be functionally similar in spite of structural differences, then the same comparison might be made between natural ecosystems. That is, we may be able to distinguish certain universal ecosystem properties measurable in all systems and, by studying these properties and their response to toxic chemicals, make inferences that would be meaningful in any ecosystem. This concept is the basis for the abstract model ecosystems originated by Beyers (described by Gorden et al. 1969) and since adapted and modified by many theoretical and applied ecologists. Such model ecosystems, consisting of a few species of bacteria, algae, and invertebrates, have no natural counterparts; in a strict structural sense, they are totally unrealistic, and yet they exhibit features such as succession, metabolic balance, and homeostasis that are characteristic of all terrestrial and aquatic ecosystems. Most people who use these experimental systems consider them to be fully valid ecosystems, to be studied just as one studies lakes, streams, and other naturally occurring ecosystems. Abstract model ecosystems have often been suggested as ecosystem-level "white rats," implying that they might be used to deduce general ecosystem properties in the same way as laboratory rats have been used to investigate the principles of mammalian physiology.

Unfortunately, the universal ecosystem properties of which we are currently aware are of little recognized social or economic relevance in themselves. The causal connections between population-level phenomena and ecosystem properties have yet to be elucidated. Thus, a chemical effect observed in an abstract model ecosystem might indicate a potential for disruption of processes in natural ecosystems, but the nature of those disruptions cannot at present be predicted.

The problem of generalizing from model ecosystem results to different natural ecosystems will remain an obstacle in system-level hazard assessment until more comparative data are available for natural systems. There are a number of substances (e.g., certain trace elements and pesticides, and petroleum products) for which dose-response observations have been made in many natural ecosystems. Such data could be compiled to provide frequency distribution curves of ecosystem sensitivity against which the sensitivity of particular laboratory ecosystem tests could be compared. Construction of such data bases represents an empirical approach to "calibrating" laboratory systems for general predictions of safe exposure levels in nature.

As a chemical progresses through the hazard assessment testing sequence, the need for general indicators of potential effects diminishes, and the need for realism in the testing situation increases. At the initial screening level, information about the relative hazards of chemicals helps determine the need for more extensive testing. A general, or abstract, model ecosystem may be useful at this stage for ranking chemicals in order of potential effects on ecosystem processes. The rankings would be expected to be more consistent among different ecosystems, and hence more generalizable, than would qualitative or quantitative predictions of effects. Thus, any laboratory system exhibiting ecosystem properties could be used to identify those chemicals with the greatest potential for affecting ecosystems. The major criterion for such a laboratory system is its ability to generate rankings that are consistent with the actual hazard potential of the chemicals in nature, rather than its ability to simulate specific ecosystem effects. Test chemicals could be compared with selected standard reference chemicals to identify those with the greatest potential for environmental effects.

Once a chemical has been indicated to be hazardous and the types of ecosystems likely to be exposed are known (through the exposure assessment process), realistic simulation becomes the major objective of ecosystem-level tests. The realism of model ecosystems is sometimes evaluated in terms of how well they "track" their natural prototypes through time. The question might be raised, how well does any ecosystem track another ecosystem? If a model ecosystem were perfected to the extent that it was identical in every measurable aspect to its natural prototype, it would be imperfect with respect to every other natural ecosystem. Since chemical hazard assessments under TSCA will usually be concerned with protecting more than a single ecosystem (although, especially in the later stages of the assessments, concern might be limited to one type of ecosystem), perfect tracking does not seem to be a reasonable criterion for realistic simulation. Rather, the "validity" of a model ecosystem could be assessed by comparing its behavior with the range of natural ecosystems. A laboratory ecosystem designed with realistic simulation as the major objective should be typical, but not necessarily identical to any particular example, of its ecosystem type.

A model ecosystem that satisfies this criterion becomes a reasonable substitute for a field experiment. When a chemical is tested in a realistic microcosm or in the field, the experiment results are scrutinized to determine which observed effects might be expected to occur in other ecosystems and which are situation-specific. Direct toxic effects on components of the test system are probably generalizable in that the same effects would occur in other situations where the same organisms receive the same exposure to the chemical. The difficulty arises in distinguishing direct toxic effects from indirect effects caused by interactions among ecosystem components. An intimate knowledge of the ecology of the test system is necessary if this distinction is to be made. Likewise, prediction of indirect effects in other ecosystems requires an understanding of the structure and function of these ecosystems as well. At present, our ability to predict indirect chemical effects in whole ecosystems is rudimentary (see Sect. 5). Results of a model ecosystem experiment are best viewed as examples of what could occur in a typical ecosystem. The predictive power of model ecosystems will depend on the growth of our basic understanding of ecosystem dynamics.

3.6.3 Potentially Useful Model Ecosystems

The number and diversity of aquatic model ecosystems is staggering. For the purposes of this review, six general categories have been selected for detailed discussion. Large, outdoor systems (e.g., Pilson et al. 1977) have been omitted as have the more complicated laboratory devices (e.g., Cooper and Copeland 1973), because construction of large numbers of replicate systems would be impractical. Other systems (e.g., Metcalf et al. 1971) have been omitted because, in the reviewer's opinion, they do not adequately represent ecosystem processes and are, therefore, unsuitable for testing chemicals for ecosystem-level effects. The six categories reviewed below range from nonrepresentational flask ecosystems to realistic simulations of natural ecosystems. Many of these systems have been used to test chemical effects, but none are so developed that a standardized test procedure has been specified. Few have been extensively compared with natural ecosystems. Therefore, "what has been done" is given less attention than "what can be done." No attempt has been made to document specific details of construction or operation of these systems; the reader is referred to the examples listed in the bibliography and to the general reviews of aquatic microcosm technique that have appeared in recent years (Warren and Davis 1971; Cooke 1977; Giddings 1980b; see also the papers contained in Giesy 1980).

(1) Mixed flask cultures. To many people, the word "microcosm" refers to a flask containing a mixed culture of bacteria, algae, and

microinvertebrates. In terms of sheer numbers of publications, mixed flask cultures are the most commonly used type of aquatic model ecosystem. Beyers was perhaps the first to use these systems for ecological research (Gorden et al. 1969). He inoculated an artificial growth medium with microorganisms from a sewage oxidation pond and maintained the cultures until a stable biotic composition was achieved. These cultures are still in existence, and the original species are still present. The organisms include several species of algae, Paramecium, a flagellate, rotifers, an ostracod, and 11 species of bacteria (Gorden et al. 1969). The strategy of inoculating artificial media with organisms collected from lakes, ponds, streams, aquaria, horse troughs (Ollason 1977), cemetery urns (Leffler 1977), and other sources appears to be consistently successful in producing simple, relatively stable model ecosystems (Bryfogle and McDiffett 1979; Cooper 1973; Kelly 1971; Kurihara 1978a,b; McConnell 1962, 1965; Neill 1972; Reed 1976; Thomas 1978; Waide et al. 1980). Gorden et al. (1969) demonstrated that these simple systems exhibit many of the properties common to all terrestrial and aquatic ecosystems (Odum 1969). They have also been used to study population- and community-level phenomena, and in a few instances, the effects of toxicants have been examined.

Because of their simplicity and small scale (usually less than 1 L), mixed flask cultures are relatively easy to mass produce for experiments with large numbers of replicates. The variablity among replicates can be minimized by cross-inoculating periodically during the first few weeks of growth. This ensures that random extinctions do not affect the composition of the community that eventually develops. Gorden (1967) noted the importance of including at least a few individuals of the larger species (particularly ostracods) in the inoculum of each culture since the presence or absence of these organisms has a disproportionate effect on the rest of the community. With these precautions, the coefficients of variation (CVs) of most measurements of ecosystem structure and function can be held below 50% (Kelly 1971; Leffler 1977). Even these values may be misleadingly high since oscillations occurring in some parameters may be identical, but out of phase among replicates, which results in high CVs at any single point in time. Waide et al. (1980) and Taub (personal communication) have attempted to overcome this problem by plotting microcosm behavior in a two-dimensional phase space with, for example, pH and dissolved oxygen levels as the two axes; identical, but out-of-phase, replicates will have identical trajectories in such a phase space.

Reproducing the same ecological characteristics from one experiment to the next is more difficult than producing good replicates within one experiment. Of course, natural sources of inocula will change between experiments. An alternative is the gnotobiotic approach (Taub 1969a,b,c; Nixon 1969), which establishes experimental communities by adding known numbers of organisms from stock monocultures. This method has the added advantage that initial population sizes may be manipulated by the experimenter. A major disadvantage is that pure stock cultures of all members of the community must be maintained; therefore, the cost in time and money of conducting an experiment is substantially increased. Another drawback of the gnotobiotic approach is that the organisms brought together in these artificial communities may not be representative of natural, co-adapted species assemblages. For this reason, gnotobiotic communities are probably not reliable for studies of ecosystem-level properties; most of Taub's research (1969a,b,c; Taub 1976; Taub and Crow 1980; Taub et al. 1980) focuses instead on population interactions.

Leffler's approach to the problem of achieving consistent results from one experiment to the next is to examine properties of mixed flask cultures that are insensitive to changes in community composition (Leffler, personal communication). Leffler is currently evaluating mixed flask cultures as screening tools for chemical hazard assessment. His strategy is to measure the effects of chemicals on a few easily measured integrative properties of the model ecosystems and to rank chemicals in order of the concentrations required to produce an observable effect. Leffler hypothesizes that these rankings will be consistent among mixed cultures with differing species composition even if the absolute values of the measured parameters are not consistent. As discussed in Sect. 3.6.2, the rankings, not the observed effects, constitute the output of this experimental design. The model ecosystems are used to identify chemicals capable of disrupting ecosystem processes, but do not specify which processes are disrupted or how these effects might be manifested in natural systems. Since many single-species bioassays have the same objective (ranking of chemicals by potential hazard), model ecosystems would be valuable primarily if they were more sensitive than conventional bioassay organisms or if they generated different rankings than those of conventional tests. If ecosystem-level screening tests merely echoed the results of simpler, more easily standardized bioassays, their use for screening chemicals would be questionable.

(2) Periphyton communities. Periphyton (also known as aufwuchs) is the community of organisms attached to or associated with benthic substrates or the submerged surfaces of macrophytes. The periphyton community includes bacteria, algae, and many kinds of invertebrates (Odum 1971). Periphyton are found in nearly all aquatic habitats. In stream ecosystems, periphyton are usually the major primary producers. They are invariably present in laboratory streams and can be a nuisance in pelagic model ecosystems (Harte et al. 1978). Although the periphyton community is only one part of an aquatic ecosystem, its functions include all the major ecosystem processes such as primary production, respiration, decomposition, and nutrient uptake, transformation, and regeneration (Rodgers et al. 1980). Periphyton communities have been used as indicators of ecosystem stress (Patrick 1973; Rodgers et al. 1980).

Periphyton communities are easily produced in laboratory systems. Typically, water from a natural stream, lake, or marine coastal ecosystem is circulated over glass slides, porcelain plates, or other artificial substrates, and organisms in the water colonize the substrates within a few days. Alternatively, an artificial medium may be used, with periphyton-covered rocks as an inoculum.

The ecology of laboratory periphyton communities has been thoroughly studied by McIntire (McIntire et al. 1964; Phinney and McIntire 1965; McIntire 1968a,b; McIntire 1973). In these systems, the species composition of the community became uniform over the substrate (gravel) within 1 month, and biomass was fairly constant after 2 to 3 months. McIntire noted that the plant communities "remained surprisingly constant" for at least 2 years, varying only in the relative abundance of species. He stated that "a well-developed periphyton community as a unit has a characteristic growth form and responds metabolically to external environmental factors [light, temperature, CO_2, dissolved oxygen, current] in a predictable way" (McIntire 1968a).

Laboratory systems for periphyton studies are usually designed in such a way that samples of the substrate can be removed for measurements of biomass, pigments, metabolism, or species abundance without disturbing the rest of the system (Bott et al. 1977; Gerhart et al. 1977; Kehde and Wilhm 1972; Kevern and Ball 1965; McIntire et al. 1964; Rodgers et al. 1980; Wulff 1971). Phinney and McIntire (1965) placed trays of substrate from the laboratory stream into chambers for measurement of photosynthesis and respiration at different temperatures and light intensities. Effects of toxicants could be studied in the same way. Replicate samples from a laboratory stream could be placed in chambers with test solutions, and effects on metabolism (Phinney and McIntire 1965; Rodgers et al. 1980) or rates of degradation of organic matter (Bott et al. 1977) could be measured over short periods of time. One stream system could provide enough replicate samples of the community for many toxicity tests, and if the community remains stable as McIntire et al. (1964) indicate that it should, experiments performed at different times would be comparable. Few other experimental systems offer the combination of stability, replicability, biotic complexity, and ease of handling found in laboratory periphyton communities.

Chronic effects of chemicals on laboratory periphyton communities have been studied by Gerhart et al. (1977) and by Rodgers et al. (1980). Whereas a single laboratory stream can supply material for many short-term tests, long-term experiments require that each stream be used for only one treatment regime. Obviously, the number of tests that can be performed by a single laboratory is severely limited. However, the stability of laboratory periphyton communities makes them ideal for chronic effects studies, providing a smooth baseline against which treatment effects can be measured. Rodgers et al. (1980) compared the variability and sensitivity of several structural and functional parameters, including dry weight, ATP, chlorophyll-a, CO_2 assimilation in the light and dark, and SO_4 assimilation in the light and dark. They found that functional measurements were much more consistent than structural measurements, and consequently, significant treatment effects were more readily detected with the functional parameters. Gerhart et al. (1977) also detected no effects on biomass or chlorophyll in their experiments, but they did observe minor (not statistically significant) changes in species abundance in communities exposed to coal leachate. They reported "excellent replicability of diatom communities" among their three control systems. No functional parameters were measured.

Results of laboratory periphyton studies, in the opinion of Kevern and Ball (1965), are consistent with ecological theory and with observations on natural systems. If light, temperature, and water flow are realistically reproduced, these laboratory systems are probably representative of natural periphyton communities. The major artificiality in laboratory systems may be the absence (in most studies) of grazers. Studies of grazer effects (Admiraal 1977; Kehde and Wilhm 1972; McIntire 1968a) have produced conflicting results, and further research in this area is warranted.

(3) Sediment cores. The sediment is the site of many important processes in aquatic ecosystems including decomposition of organic matter, nutrient regeneration, and degradation of contaminants. Exchanges between the sediment and the overlying water play a major role in nutrient cycles and in controlling chemical conditions in lakes and marine environments (Golterman 1976; Hutchinson 1975; Mortimer 1941, 1942; Pomeroy et al. 1965). Because processes occurring in the sediment and at the sediment-water interface are difficult to measure in situ, the technique of extracting sediment cores with overlying water for study in the laboratory has been widely used by ecologists. If cores are maintained at ambient temperatures, with aeration and mixing of the water to simulate natural conditions, ecological processes and effects of chemicals can be examined over extended periods of time. The methodological approach is essentially identical for studies in hypolimnetic, littoral, or coastal marine environments.

Sediment cores, unlike terrestrial soil cores (Sect. 4.2), have not been used extensively in research on chemical contaminants. The following discussion is based on work performed at EPA's Gulf Breeze Environmental Research Laboratory (Pritchard et al. 1979) and at the Utah Water Research Laboratory at Utah State University (Porcella et al. 1976). Much of the information presented here comes from personal communications with H. P. Pritchard (Gulf Breeze ERL) and Allen Medine (formerly of Utah State University, presently at the University of Connecticut). An outline for a chemical testing protocol using sediment cores was formulated by these two scientists at the Workshop on Methods for Measuring Effects of Chemicals on Aquatic Ecosystem Properties held in conjunction with this project (Giddings 1981).

The Gulf Breeze cores are extracted intact from an estuarine salt marsh. They are used primarily in short-term (up to 21 days) studies of microbial degradation of organic contaminants. Because of the relatively short duration of the experiments, semicontinuous replacement of the overlying water is not necessary. Like Medine's microcosms, the Gulf Breeze cores are sealed, and various chemical measurements can be made on the air leaving the systems. Although these microcosms are designed for degradation experiments, Pritchard believes that they could be used to study the effects of chemicals on microbial communities and possibly (if larger cores were used) on benthic invertebrates.

Medine and Porcella's systems consist of homogenized lake sediment, artificial medium, and a gas phase. The sediment is homogenized to promote uniformity among replicate systems. An artificial medium is used to facilitate mass balance calculations; 10% of the water volume is replaced each day. The systems are completely sealed so that gas production and consumption in the microcosms can be measured. Cores are illuminated to simulate shallow littoral habitats or darkened to simulate hypolimnetic regions. These cores can be used to measure the effects of chemicals on major biogeochemical cycles (C, N, S) including denitrification and N-fixation, microbial respiration, organic matter decomposition, primary production (in illuminated systems), and species diversity. Both Medine and Pritchard report good agreement among replicate cores.

A number of experimental factors have been found to influence the behavior of sediment cores. Medine emphasizes the importance of sediment and water characteristics on measured variables, especially nutrient exchange across the sediment-water interface. Pritchard notes that the microbial activity in his systems is affected by the dimensions of the core, the water:sediment ratio, and the sediment surface area. The Gulf Breeze researchers have also investigated the effects of homogenizing the sediment and observed that cores with homogenized sediments degrade some organic chemicals faster than intact cores, at least over 8 to 15 days. Medine's experiments run for several months, and it is conceivable that the stimulation of microbial activity caused by mixing the sediment disappears once the initial flush of nutrients is exhausted.

The sediment core technique could be applied at almost any level of a hazard assessment scheme. Simple static systems like the Gulf Breeze cores are amenable to short-term tests of chemical effects, whereas Medine's complex semicontinuous flow cores are suitable for long-term studies. The Gulf Breeze researchers have also experimented with continuous-flow, sediment-water systems for long-term degradation experiments. Intact cores with natural water should provide realistic sitespecific simulation for short experiments. Realistic simulation is probably not possible over long periods (Pritchard), but even homogenized cores with artificial medium can reproduce the general features of natural sediments (Medine). Sediment cores definitely merit further development as hazard assessment tools.

(4) Pelagic microcosms. The pelagic zones of lakes and coastal ecosystems present serious problems for microcosm simulation. The structure and function of pelagic ecosystems are strongly influenced by water movements, which carry planktonic organisms up and down in the water column (thereby exposing them to a range of nutrient and light regimes) and resupply the surface water with nutrients from the bottom water and the littoral zone (Nixon et al. 1980). Currents also transport plankton communities horizontally, bringing them into contact with other patches containing different organisms and different nutrient conditions (Margalef 1968). Enclosure of a pelagic system alters the vertical distribution of organisms and dissolved substances, cuts off nutrient inputs, and creates homogeneity in the place of patchiness. Primary production per unit volume of a phytoplankton community is usually low in pelagic microcosms; thus, fish are difficult to maintain without seriously altering community structure (Jassby et al. 1977b). Pelagic ecosystems are inherently variable and unpredictable, and pelagic microcosms are no less so (Giddings 1980).

Many aquatic ecosystems can be satisfactorily reproduced in the laboratory if natural physical conditions are simulated (Giddings 1980). Perez et al. (1977) attempted to duplicate the physical conditions of lower Narragensett Bay in 150-L pelagic microcosms. The microcosms were stirred with paddles to create turbulence equal to that of the bay, as measured by dissolution rates of hard sugar or gypsum. Microcosm water was replaced with bay water semicontinuously at a turnover rate approximately equal to that of the bay. The natural temperature regime was maintained by pumping bay water through a water bath around the microcosms. The natural photoperiod was reproduced. Experiments with light intensity are discussed later. A small benthic component was included in each microcosm, consisting of an intact sediment core in an opaque box through which microcosm water was circulated at a rate approximating that estimated for the bay. The ratio of sediment surface area to water volume was equal to the overall surface/volmume ratio of the bay. In short, an effort was made to establish conditions in the laboratory as close as possible to estimates or measurements from the natural ecosystem.

In their first experiment, Perez et al. (1977) found that, when the average light intensity in the microcosm water column was equal to the estimated average light intensity in the bay water column, an algal bloom occurred. Reasons for this bloom are still unknown (Perez, personal communication). Because grazers were more abundant in the microcosms than in the bay, the bloom probably did not result from reduced grazing. Release from nutrient limitation is a possibility; nitrogen concentrations in the bay water were quite high, but phosphorus (which was not measured) may have limited algal growth in the bay. Whatever the cause, Perez found that the bloom could be prevented by reducing the light intensity to 15% of that in the bay water column. Although imposing light limitation succeeded in holding algal growth in check, the fact that light levels were many times higher in the bay implies that the natural algal community was not light-limited. Consequently, subsequent experiments on the effects of turbulence, water turnover time, and sediment surface area are difficult to interpret. This research demonstrated the difficulty of simulating pelagic conditions in laboratory microcosms.

Because exchange rates of nutrients, organisms, and suspended material between the pelagic and benthic components were a major uncertainty in the original design, Perez is now developing a modification of the benthic-pelagic coupling in these microcosms. The modified systems will include a sediment core and a 1-m water column set up alongside the pelagic tank; turbulence near the sediment surface and exchanges with the pelagic portion will be under direct experimental control (Perez, personal communication). For chemical testing, Perez has constructed pelagic microcosms entirely of glass. The fate, transport, and effects of radio-labelled 2-ethyl-hexylphthalate were studied in a series of experiments lasting 30 to 90 days each. Perez reports good replicability in these experiments for measurements related to the fate and transport of the chemical, with more variability in measurements of phytoplankton, zooplankton, and bacteria (Perez, personal communication). He concludes that pelagic microcosms are useful for intensive studies of chemicals of particular interest, but are impractical for screening.

Researchers at Lawrence Berkeley Laboratory (LBL) have experimented with freshwater pelagic microcosms for several years (Dudzik et al. 1979; Jassby et al. 1977a,b; Harte et al. 1978, 1980). These microcosms are 50- or 700-L tanks containing natural water or artificial medium and a naturally derived lake plankton community. Turbulence is created by gentle aeration. There is no water replacement and no benthic component (the latter will be included in future experiments; J. Harte, personal communication).

A serious problem encountered in the early work with these microcosms was the growth of periphyton on the walls of the tanks. After several months of operation, the chemistry and biology of the systems were dominated by the periphyton, making realistic simulation of pelagic conditions impossible. Attempts at mechanical and biological control of side growth were ineffectual. The researchers concluded that the microcosms were most useful in the early stages of community development (before periphyton growth became significant), which were likened to the seasonal blooms observed in most temperate lakes (Dudzik et al. 1979; Harte et al. 1980; Jassby et al. 1977a,b). Eventually, a strategy of periodic transfer of the cultures to clean vessels proved successful in avoiding the periphyton problem (Harte et al. 1980). Perez (personal communication) eliminates wall growth in his pelagic marine microcosms by scraping the walls daily.

The LBL microcosms were used to test a technique for predicting the sensitivity of lakes to stress. The sensitivity prediction was based on the response of a sample of the pelagic community to organic enrichment. Microcosms with different initial nutrient levels were constructed and monitored for 2 months. The sensitivity of the microcosms was assessed by using the organic enrichment method, and the systems were then treated with ammonium, iron, or phenol and monitored for another 2 months. The predicted sensitivity of each type of system was compared with the actual response of the system to perturbation. The features measured in the microcosms included phytoplankton and zooplankton populations, nutrient concentrations, and (in some experiments) diurnal pH changes for estimation of primary productivity. The authors concluded that taxonomic enumeration was best able to characterize the response of pelagic microcosms to stress (Harte et al. 1978, 1980). Nutrient concentrations were insensitive to the chemical perturbations, possibly because of the disproportionate influence of periphyton on the water chemistry. Productivity estimates were sometimes difficult because the small pH changes could be detected only by measurements too precise for most instruments (Harte et al. 1978).

Microcosm research at LBL is progressing in three areas. First, tracking studies have been undertaken to compare pelagic microcosms with the natural lake ecosystems from which they were derived. It has been found that the phytoplankton community dynamics of the microcosms can be made to approximate those of the lake for up to 2 months if (1) the natural temperature regime is reproduced and (2) microcosm wall growth is controlled. A second area of research is the extension of Perez's benthic-pelagic coupling to freshwater systems. Finally, experiments on chemical effects are continuing, with the emphasis on interactions between chemicals and organic enrichment, and on the resulting alterations in decomposition rates and nutrient cycling (Harte, personal communication).

Considerable work remains before the applicability of pelagic microcosms to chemical hazard assessment can be determined. If detailed plankton counts are necessary for evaluating the response to chemicals, then these systems are not practical for testing large numbers of chemicals. The labor required for species enumeration is excessive, and special training in plankton identification is required. The replicability of plankton counts is generally poor (Harte et al. 1978). Reproducing species dynamics from one experiment to the next may be difficult. In addition, the true significance of population changes is not apparent, since major shifts in plankton communities can occur without altering community functions (Harte et al. 1980; O'Neill and Giddings 1979).

Attention must be given to measurements of ecosystem properties in pelagic microcosms. Production and respiration should be fairly easy to monitor in these systems by measuring diurnal fluctuations in dissolved oxygen. Various approaches to detecting chemical effects on nutrient cycling were described in Section 3.6.1. Further development of pelagic microcosms for chemical assessment is proceeding along these lines at LBL. Comparisons between pelagic microcosms and natural pelagic ecosystems should address these ecosystem-level properties instead of, or in addition to, the taxonomic structure of the plankton community. Strategies for improving the ability of microcosms to simulate natural pelagic ecosystems must be devised. In their current state of development, pelagic microcosms are useful tools for basic research and some special applications, but they are not yet ready for standardization as TSCA hazard assessment protocols.

(5) Pond microcosms. The development and characterization of pond microcosms has been the objective of a research program initiated at Oak Ridge National Laboratory (ORNL) in 1975. Very similar model ecosystems have been under study at EPA's Athens Environmental Research Laboratory (Brockway et al. 1979) and have been included in the chemical environmental assessment program of the Monsanto Company (Eggert et al. 1979; Gledhill and Saeger 1979). The evaluation presented in this section is based primarily on the results of the ORNL study (Harris et al. 1980).

Of all natural aquatic ecosystems, shallow ponds are the least distorted by encapsulation under laboratory conditions. Mature pond microcosms are ecologically quite similar to temperate ponds in mid-summer. The dominant pond plants and animals (except fish, in most cases) thrive in pond microcosms. Microcosm periphyton and sediment communities contain the same taxonomic groups in roughly the same proportions as natural ponds. Water chemistry in microcosms is often similar to the parent ecosystem even after months in the laboratory. Most importantly, effects of chemical perturbations in ponds appear to be reproduced accurately in pond microcosms. One reason for this realism is that the physical conditions characteristic of ponds (shallow depth, lack of turbulence) are easily reproduced in aquaria. Another is that virtually all of the important ecological components and processes of whole pond ecosystems can be included in microcosms. This is not true for other aquatic ecosystem types, which must be broken down into subsystems (such as periphyton, sediment, or plankton) for study. Consequently, results of pond microcosm studies can be applied to natural systems with fewer assumptions and extrapolations than results derived from other experimental systems.

The pond microcosms developed at ORNL, Athens, and Monsanto are all derived by placing natural sediment, water, and samples of natural pond communities into aquaria and allowing the systems to evolve. The communities undergo a succession exhibiting many universal features of ecosystem development (Odum 1969) and culminating in a well-regulated system in which chemical and biological meaurements fluctuate within narrow limits. Although the exact course of succession may differ among replicate microcosms and between experiments, the mature communities are usually very similar. Coefficients of variation among mature replicates are below 20% for most measurements, particularly production, respiration, and the P/R ratio (Brockway et al. 1979; Giddings and Eddlemon 1979; and references cited therein). Pond microcosms can remain in this stable, reproducible condition for many months and are thus ideal for studies of chronic effects of chemicals on whole ecosystems.

Pond microcosms are extremely simple to construct and operate. The fact that three laboratories have independently established similar experimental protocols for microcosm experiments is evidence of this. The microcosms designed by these laboratories are ecologically very similar despite different source materials. Thus, we conclude that the technique could be used successfully in any laboratory, with the quality of results dependent mainly on accurate measurements and analyses rather than on system design.

The research groups at Athens and Monsanto have used pond microcosms primarily for studies of chemical transport and degradation. The ORNL program originally had similar objectives, but it was realized that the microcosms could also be used to measure ecosystem-level effects. Experiments have been conducted on the effects of arsenic (Giddings and Eddlemon 1978, 1979; Harris et al. 1980) and a coal-derived oil (Giddings 1979). A second, more comprehensive experiment with a synthetic oil began in August 1980 and will be followed by an experiment with the same material in outdoor ponds; this combination of studies should permit a thorough evaluation of the utility of pond microcosms for predicting effects in larger systems. *Based on results obtained so far, our tentative conclusion is that effects can be realistically simulated in the laboratory systems. The principal question that remains is not, "Do pond microcosms accurately represent ponds?", but rather, "To what extent are ponds representative of other aquatic ecosystems of interest?"*

Pond microcosms would not be convenient for screening large numbers of chemicals--experiments require too much time (about 2 months to reach maturity) and space. They could be extremely useful at intermediate and upper levels of a hazard assessment program. The hazard evaluation process at Monsanto incorporates pond microcosms for predictive and confirmative studies after initial screening with simpler systems (Gledhill and Saeger 1979).

(6) *Model streams*. To a much greater degree than other ecosystems discussed above, streams are open systems in which processes occurring at a given point influence conditions downstream. Energy and nutrient fluxes in streams may be more "spiral" than cyclic (Webster 1978). Therefore, the ecosystem really includes the entire length of the stream from headwater to mouth. For this reason streams are, in the opinion of Warren and Davis (1971), "among the most difficult freshwater systems to model." Critical parameters in the design of model streams include inflowing water quality (especially nutrient levels and organic content), bottom type, depth, current velocity, temperature, and light (Warren and Davis 1971).

Participants in the Workshop on Methods for Measuring Effects of Chemicals on Aquatic Ecosystem Properties (Giddings 1981) recognized three major classes of model streams: closed (completely recirculating) systems, partially recirculating systems, and open (once-through flow) systems. These system types generally fall along a gradient from small, completely recirculating laboratory devices to large-scale outdoor streams. The smaller, recirculating model streams are easier to construct and operate, are less expensive, and require less laboratory space than the larger systems. The methodology of smaller systems is also more easily transferred to other laboratories than larger systems. In the opinion of the workshop participants (Giddings 1981), statistical analysis of results is easiest with small model streams. The inherent variability of larger models means that more samples are needed to achieve a given level of confidence in the measurements and that temporal trends are more difficult to detect. Finally, responses to chemicals are more easily interpreted in small systems, where cause and effect are more easily distinguished than in complex systems. Because of these factors, simple laboratory recirculating streams come closest to satisfying the operational criteria for a TSCA hazard assessment tool.

However, the same systems that are most amenable for routine chemical hazard assessment may be the least generalizable to natural ecosystems. Small recirculating model streams lack the openness that is the distinctive feature of stream ecosystems; only larger, open systems are enough like natural streams to permit reliable predictions. Even with larger model streams, doubts about ecological realism were expressed by participants in the workshop (Giddings 1981). Because of the difficulty of reproducing the structure and function of stream ecosystems, model streams may be most useful for studies at the organism or population level. Warren and Davis (1971) mention many potential research applications, including studies of animal behavior, habitat selection, food selection, territoriality, predation, and competition. Studies of community structure, ecosystem metabolism, diversity, and stability are not recommended since factors controlling these properties may or may not be included in the model system (Giddings 1980).

Our conclusion is that model streams, while potentially useful in many areas of applied and basic ecological research, are not promising for chemical hazard assessment under TSCA. At best, they might be employed in advanced stages of testing when transport and fate have been fully characterized and probable ecological effects have been carefully defined. In such cases, the model ecosystems must be specifically designed to incorporate the processes and components relevant to the questions being asked.

3.6.4 Conclusions and Recommendations

The relevant characteristics of the model ecosystem types discussed above are summarized in Table 3.1. The second column

TABLE 3.1. CHARACTERISTICS OF MODEL ECOSYSTEMS

System type	Ability to replicate	Realism	Generality	Potential application
Mixed flask culture	High	Low	High?	Screening
Periphyton community	Med-high	Med-high	Medium?	Intermediate or advanced testing
Sediment core	Med-high	Medium	Medium?	Intermediate or advanced testing
Model ponds	Medium	High	Medium?	Intermediate or advanced testing
Pelagic microcosms	Low-med	Low-med	Medium?	Research
Model streams	Low	Low-med	Medium?	Research

heading in this table, "Ability to Replicate," refers to all aspects of constructing and using many replicate test units. Variability among replicates (largely a function of the response being measured) is one factor included here. "Realism" implies the ability of the model ecosystem to simulate a particular natural ecosystem, and "generality" was discussed in Sect. 3.6.2. Without a great deal more comparative data on aquatic ecosystem functions and responses to chemicals, generality is difficult to evaluate for any model ecosystem; the entries under this heading are highly subjective and likely to change as our knowledge improves.

The only model ecosystem potentially efficient enough for routinely testing large numbers of chemicals is the naturally derived mixed flask culture. If these systems are found to be more sensitive to chemicals than conventional assays, the ecosystem tests could replace certain less sensitive and less efficient single-species tests such as the algal growth test. If the model ecosystem tests rank chemicals differently from conventional tests (that is, if ecosystem-level hazards are not predictable from single-species bioassays), mixed flask cultures could be used in conjunction with the existing battery of tests. Either of these possibilities is contingent on the outcome of the ecosystem tests being relatively independent of the system's species composition since any particular taxonomic structure may be difficult to repeat exactly in successive experiments.

Sediment cores, periphyton communities, and model ponds are all potentially useful in intermediate or advanced stages of hazard assessment. Model ponds require more time and space than the other two systems and are, therefore, somewhat less efficient for routine testing. Sediment and periphyton systems also have the advantage that they can be applied to almost any aquatic ecosystem. Model ponds, on the other hand, are whole ecosystems, whereas the sediment and periphyton systems represent only parts of whole ecosystems. Model ponds are the most realistic type of model ecosystem. All three of these laboratory systems merit further development. Strategies need to be developed for making these systems as widely representative as possible.

Pelagic microcosms and model streams are still too unwieldy and unpredictable for use as TSCA testing tools. They are neither as efficient nor as realistic as model ponds, but they have been quite useful for basic ecological research and could be of value for special applications in chemical testing.

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LABORATORY TESTS FOR CHEMICAL EFFECTS ON TERRESTRIAL POPULATION INTERACTIONS AND ECOSYSTEM PROPERTIES

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SECTION 4

LABORATORY TESTS FOR CHEMICAL EFFECTS ON TERRESTRIAL POPULATION INTERACTIONS AND ECOSYSTEM PROPERTIES

The potential multispecies laboratory test systems discussed in this section were selected on the basis of a literature review and workshops on population interactions and ecosystem properties (Suter 1980a, b). Highest priority was given to systems that had been used for testing effects of chemicals. Somewhat lower priority was given to systems that were well studied and documented, but that were designed for such uses as pure research or studies of chemical transport. Lowest priority was given to systems that had (1) been little studied or (2) had not been studied at all as complete laboratory systems, but that had been suggested by one of the workshop panels.

Potential test systems are identified and evaluated in the text of this section and in Appendix B. The criteria used for test evaluation include (1) the state of development of a system, (2) sensitivity of the system, (3) ability of the system to simulate responses in the real world, (4) the ecological and economic importance of the organisms and processes included, (5) cost, (6) technical difficulty, (7) the availability of system components, (8) the range of responses displayed by the system, and (9) the time to response.

Multispecies test systems should be included in a chemical hazard assessment scheme because of (1) the effects of ecological systems on the activity of test chemicals, (2) the effects of the system context on the responses of the individual components, and (3) the effects of chemicals on holistic properties of systems.

Ecological systems may affect the activity of a test chemical by chemically or physically transforming it, by concentrating or diluting it, or by changing its availability. The soil microflora may degrade or detoxify a chemical or may even increase toxicity through partial oxidation. The soil itself may affect the availability and toxic properties of a chemical by sorption and abiotic oxidation and reduction. Higher organisms may take up chemicals and partially or completely metabolize them, sequester them in relatively inactive tissues such as the cuticle, or pass them to exploiters in a concentrated form.

The response of an individual organism or population to a chemical may be modified by its interactions with other system components. For example, chemicals may affect the ability to avoid predation, find prey, compete, or subsist on toxic or marginally nourishing hosts. Because interactions between organisms often result in stress or increased energy expenditure, traditional response parameters may be more sensitive to chemicals in multispecies systems. Because interactions of organisms or populations require behavioral and physiological responses which are not displayed in isolation, the range of measurable responses to a chemical is greater in multispecies than in single species systems. Therefore, the responses of the individual components in a multispecies test system may be both more realistic and more sensitive than if that component were tested alone.

Holistic properties, those which are characteristic of an entire hierarchical level of organization, can measurably respond to test chemicals. These include collective properties which are summarizations of the properties of system components and emergent properties which are not summarizations of the properties of components (Salt 1979). Collective properties such as diversity, foodweb connectivity, and community production and respiration provide indices of the state of the system. In many cases, the responses of these collective properties have greater practical importance than the responses of the individual component organisms or populations (e.g., soil respiration is more important than the respiration of any individual microbial population). Collective properties can be no more sensitive than the most sensitive component, but they can be considerably less sensitive. Functional or numerical replacement of sensitive species by insensitive analog species can result in the masking of toxic effects when collective properties are measured (O'Neill and Giddings 1979). This structural and functional redundancy is, however, a property of natural systems and does not invalidate the use of collective properties as indicators of the effects of chemical on communities.

Emergent properties are often attributed to communities and ecosystems on the basis of loosely supported teleological arguments or loose definitions of emergence. Emergent properties are probably uncommon in communities and ecosystems because selection has relatively little opportunity to act on these higher organizational levels (Salt 1979). The replacement rate of communities is very low relative to those of populations within a community and individuals within a population so that selective pressure is less intense at higher organizational levels. In addition, community-level selective pressure must act in the face of gene flow to the constituent populations from other communities. Recent successes in predicting the properties of communities with models based on the properties of populations (O'Neill and Giddings 1979; Shugart and West 1980) suggest that emergent properties need not be invoked at the community and ecosystem level.* Therefore, the only emergent properties which appear to be testable in multispecies systems are those associated with interactions of pairs of coevolved species such as the formation of nodules by legumes and rhizobia and of lichen thalli by algae and fungi.

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*A less restrictive definition of emergent properties is used in systems theory. The components of such systems (e.g., transitors or plant populations) are treated as having properties which are independent of the system into which they are assembled. The system merely reduces the range of behavior of the components. The emergent

4.1 Population Interactions

This section is organized according to competition, predation, and the other conventional classes of population interactions. This organization is not meant to imply that tests can be developed to represent these interactions in the same sense that rats serve to represent mammal species of varying sensitivity. The class Mammalia is composed of organisms that share a large number of physiological processes, but the class of interactions called competition, for example, has no mechanistic commonality. Exploitation competition consists of division of a limiting resource (Park 1954), which can occur by a contest or scramble (Nicholson 1954). Interference competition (Park 1954) consists of the many other mechanisms by which one organism reduces another organism's use of a limiting resource including allelopathy, interspecific territoriality, predation, and physical contact. The large number of distinct mechanisms of interaction, which are called competition because they share a common outcome, are unlikely to respond in a qualitatively similar manner to chemical substances. Similar arguments can be made concerning predation, symbiosis, herbivory, and parasitism.

This problem is not serious for tests that are used only for screening chemicals and not for predicting specific effects. Screening tests only need to be sensitive to a wide range of chemicals and to produce a representative relative ranking of toxicity. The outcome of many population interactions is highly sensitive to normal ecological variables, and it seems likely that they would also be more sensitive to chemicals than a single-species bioassay. This supposition has rarely been tested, however, and is not always supported by the evidence (e.g., Kochhar et al. 1980). This use of population interaction tests would, like the use of second stressor in bioassays, simply be a method of increasing or broadening sensitivity

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properties of systems theory (e.g., signal amplification or community biomass) are simply a result of the topology of the system (Caswell et al. 1972). If this general model is as correct for ecosystems as for electrical circuits, ecosystems have no emergent properties in Salt's (1979) sense. Predictions of effects of toxicants on ecosystem properties are made on the basis of individual responses of individual organisms which are assumed to be independent of the system context (e.g., West et al. 1980). Emergent properties according to systems theory require better models rather than better tests (see Sect. 5).

over that of a standard, single-species test. Development of multispecies test systems simply for their sensitivity is not recommended.

Predictive tests (those that actually predict responses in the field) are necessary to establish the significance of responses observed in screening tests. For this purpose, tests must be representative of classes of interactions that are economically or ecologically important and yet are so narrowly defined as to encompass a generally uniform set of response mechanisms. Examples of these tests might include predation by hymenopteran parasitoids and herbivory by homopterans.

Another general problem concerns the definition of a population interaction test system. Because the results of population interactions are defined in terms of changes in population size and composition, the test systems must allow completion of multiple life cycles by each component species. This requirement might be circumvented in many instances by developing predictive indicators of response. One strategy is to use experimental designs and mathematical models that permit the prediction of outcome from data on a single generation, such as those developed for competition by DeWit (Sect. 4.1.1). Another strategy is to isolate components of the interaction that are both sensitive to toxicants and important to the outcome of the interaction, such as (possibly) predator searching efficiency or photosynthesis rates of competing plants. Finally, stress symptoms such as reduced larval size in competing Drosophila may provide early indicators of the ultimate outcome of the system.

Test systems developed using these strategies would only be indicative of effects on population interactions and not truly predictive because they inevitably ignore some components of the interaction. Tests of predator searching, for example, typically treat the prey as passive fodder. All test systems that do not include numerous generations exclude the possibility of evolutionary responses. It will be important to determine the magnitude of error induced by simplifying the interactions relative to errors induced by extrapolating between different groups of interacting species and by extrapolating from the laboratory to the field.

4.1.1 Competition

"Competition occurs when a number of animals [or plants] (of the same or different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when animals [or plants] seeking that resource nevertheless harm one or the other in the process" (Birch 1957). As indicated in Sect. 4.1, this widely quoted definition of competition includes a broad variety of mechanisms of interaction, more than one of which is often involved in a particular two-species interaction. Operationally, competition is said to occur when the fitness of one population is reduced by the presence of another population that uses a common resource.

Different approaches to the analysis of competition have developed. Because Park's Triboleum competition system [Sect. 4.1.1 (2)] invariably results in extinction of one species, the response of this system is expressed in terms of time to extinction and is modeled by a stochastic version of the Lotka-Voltera competition equations (Leslie 1958). Results from competition systems that are stable (i.e., do not lead to extinction) or that cannot be carried to termination because of the long generation times of the organisms involved have results expressed as changes in relative frequency. These are analyzed in terms of DeWit's (1960) ratio diagrams (Fig. 4.1). Data are fit to the model:

$$\log (O_1/O_2) = \log \alpha + \beta \log (I_1/I_2),$$

where O_1/O_2 is the ratio of the output frequencies of the two species, and I_1/I_2 is the ratio of the input frequencies. The intercept (log α) provides a measure of the fitness differential when the input ratio equals 1, whereas β measures the change in relative fitness with varying input frequency. A line with a slope of 1 [Fig. 4.1 (line a)] indicates that fitness is independent of the relative frequency, and one species will become extinct. A line with a slope <1 [Fig. 4.1 (line b)] indicates that the less frequent species is favored, and a stable equilibrium frequency exists at the intersection of the fitted line with the diagonal. A slope >1 [Fig. 4.1 (line c)] indicates that the more frequent species is favored, and the equilibrium is unstable. Maximum likelihood methods provide a more efficient analysis of this model than the traditional least squares regression (Adams and Duncan 1979). The experimental design used with this analysis is the replacement series. The total input density is kept constant, and the ratio of the two species is varied (e.g., 0:5, 1:4, 2:3, 3:2, 4:1, 5:0).

(1) Microbial competition. Microbial competition has received considerable attention. However, nearly all such work has been performed using liquid culture (Alexander 1971; Fredrickson 1977; Meers 1973) because the use of soil greatly inhibits the extraction, identification, and enumeration of microorganisms. Studies that realistically address competition in the soil (e.g., Rennie and Schmidt 1977) require elaborate techniques such as the fluorescent antibody technique. Because of this problem, tests for effects on microbial competition should be limited to liquid cultures that simulate aquatic systems. Further, interest in soil microorganisms primarily concerns the processes that they perform rather than the species performing them. Microbial processes are discussed in Sect. 4.2.

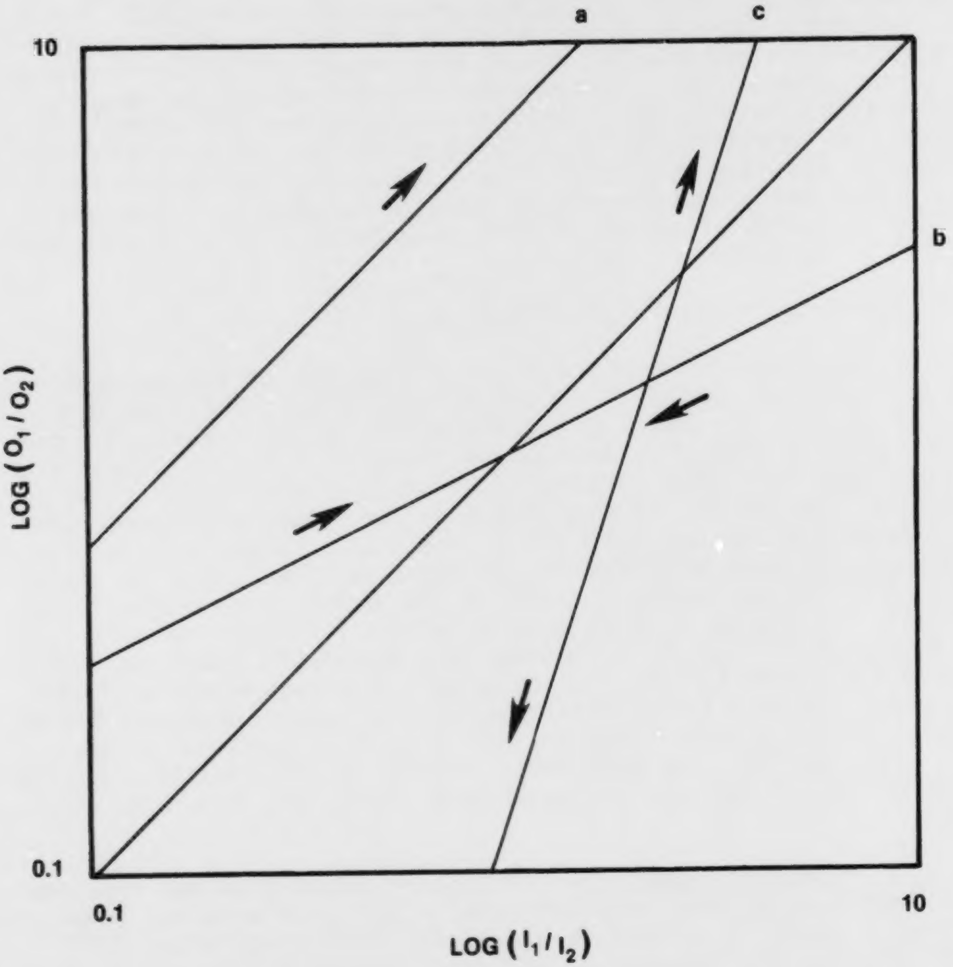

FIGURE 4.1· RATIO DIAGRAM: I_1 / I_2 = THE RATIO OF THE INPUT FREQUENCIES OF SPECIES 1 AND 2 AND O_1 / O_2 = THE RATIO OF OUTPUT FREQUENCIES.

(2) Plant competition. Because autotrophic plants lack the diverse resource base and behavioral repertoire of heterotrophic organisms, plant competition is both intense and mechanistically limited. Plants engage in exploitation competition for space (light), water, and mineral nutrients. Interference competition between plants primarily involves allelochemicals released as leachates from living or dead tissues or as root exudates. The hypothesis that plant competition is a relatively uniform process is supported by White and Harper's (1970) determination that a wide variety of combinations of plant species in the field and laboratory give a good fit to the equation of Yoda et al. (1973) for the relationship of weight (w) to density (p) in self-thinning communities: $w = cp^{-3/2}$, where c is a constant.

Socially important plant competitors include weeds and crops, more and less commercially desirable species of trees, and components of mixed-species crop and pasture systems. Some pairs of plant species such as mixed barley and oat crops (DeWit 1960) engage in pure exploitation competition [Fig. 4.1 (line a)]. Apparent stable equilibria due to rare species advantage include species of Avena (Jain 1969) and Papaver (Harper and McNaughton 1962). Interference competition could be demonstrated using any allelopathic plant (Rice 1974 and 1979). Allelopathy could result in an advantage to the more common species [Fig. 4.1 (line c)].

Competition between pasture grasses and legumes is a relatively well-studied system that is also commercially important. Clover-grass mixtures are frequently used in seeded pastures to maximize yield and nutritional quality of the pasture. Bennett and Runeckles (1977) found that 0.09 ppm ozone changed the crimson clover-annual ryegrass competitive balance from favoring clover to favoring ryegrass. Kochhar et al. (1980) found that ladino clover growth was reduced by fescue competition and by 0.03 ppm ozone, but the combination of ozone and fescue produced no greater growth decrement than either factor produced alone. However, leachate from ozone-exposed fescue, but not control fescue, inhibited clover nodulation. While the differences in the results of these two studies may be attributable in part to differences in experimental design and techniques, they suggest that generalization may be difficult even between closely related systems. A tentative protocol for a clover-grass competition test is presented in Suter (1981a).

Alternative candidates for plant competition exist in profusion. Competitors could be chosen to represent taxonomic groups (i.e., monocot-dicot) life forms (i.e., tree-herb or annual-perennial) or community types (i.e., tilled agriculture or old field). Which of these organizational schemes would provide the strongest basis for predictive generalization is not clear.

Plant competition tests should be designed as replacement series with at least three ratios (each species alone and an equal mix).

Plants would ideally be grown to maturity because of differences in responses to chemicals in different phenological stages and the importance of effects on production of propagules. Nevertheless, shorter tests have some applicability because vegetative biomass of immature plants is the parameter of interest in many managed systems. Competitive outcomes measured by harvesting vegetation can be analyzed in terms of relative yield (r = the yield of a species in the mixture/monoculture yield), total relative yield (RYT = $r_1 + r_2$), and the crowding coefficient ($k_1{}'_2 = r_1/r_2$).

(3) *Arthropod competition*. The arthropod competition systems discussed below represent over 90% of the laboratory studies of terrestrial arthropod competition. They are all saprophytic systems. Competitive interactions between herbivores have received relatively little attention. Any herbivorous arthropod that is a significant competitor of a pest species is likely to be a pest itself. Although damage may be somewhat reduced by interference competition between pests, there are no positive outcomes from such competition, and therefore it has little appeal to management-oriented entomologists. Competition between predators, and particularly among parasitoids, has important effects on the success of biocontrol. Therefore, these interactions have been somewhat better studied. Arthropod herbivore, predator, and parasitoid competition are discussed in Sects. 4.1.2 and 4.1.3(2).

(a) *Drosophila*. The members of the genus *Drosophila* are among the most studied organisms in biology. Hundreds of papers have been published on competition among more than a dozen species of *Drosophila* over a period of 45 years (beginning with L'Heritier and Teissier 1937). Because this work has been dominated by population geneticists, emphasis has been placed on the evolution of fitness under competition. The response of *Drosophila* competition to chemicals has not been studied.

Depending on the pair of *Drosophila* species and physical conditions chosen, a particular species may become extinct. This species may be indeterminant (Barker and Podger 1970; Miller 1964), or both species may coexist indefinitely even though they occupy the same niche by the criterion of the Lotka-Voltera competition equations (Ayala 1970, 1971). Coexistence can be explained by an increase in fitness with decreasing frequency [Fig. 4.1 (line a)] or by evolved shifts in competitive advantage. Complete shifts in dominance have been observed in competition between *D. melanogaster* and *D. simulans* (Moore 1952) and between *D. serrata* and both *D. pseudoobscura* and *D. melanogaster* (Ayala 1966), supporting the evolutionary model. Relatively stable frequency ratios that support the DeWit model of frequency dependence have been obtained using the following pairs: *D. pseudoobscura* and *D. willistoni* (Ayala 1971); *D. pseudoobscura* and *D. serrata*; and *D. nebulosa* and *D. serrata* (Ayala 1969). These stable frequencies are achieved with varying input frequencies.

Drosophila experiments have traditionally been conducted in 250-mL or smaller bottles or vials with a yeast-containing medium covering the bottom. Various alternative container designs that offer some advantages in manipulation have been used, but none of them are widely accepted. Media, vials, anesthetizing equipment, and some *Drosophila* species and a large variety of mutant types are commercially available. The use of flies with conspicuous genetic markers makes sorting relatively easy.

Although the number of adult flies of each species is the standard parameter in *Drosophila* competition experiments, a variety of other parameters, including stage-specific viability, length of stages, weight of adults, wing length, and the ratios of numbers, weights, and development times of males and females, have been used. All these parameters have been shown to respond to the effects of competition, but their response to chemicals is unknown.

The utility of *Drosophila* competition as a screening test is suggested not only by the sensitivity of the outcome to temperature, light, and other physical parameters, but also by its response to radiation. Moth and Barker (1977) found that viability of flies was significantly reduced by 35 µCi of ^{32}P in 30 mL of medium. Blaylock and Shugart (1972) found that treatments of 250 and 500 rads, but not 1000 rads, increased the fitness of inbred *D. simulans* in competition with inbred *D. melanogaster*. They concluded from this and previous studies that low levels of radiation in a largely homozygous population results in heterosis, but at high levels the effects of deleterious genes predominate. Because *Drosophila* species have been shown to coexist in the field in fruit, oak fluxes, and fungi (Atkinson 1979; Budnik and Brncic 1974), this laboratory system represents a natural phenomenon. The outcome of competition among *Drosophila* or other saprophagic flies is not, however, of such importance that a predictive test system is desirable.

A *Drosophila* competition test might be simply based on changes in relative frequency after one generation at one frequency. This test would only require a few small vials, and by using *D. melanogaster* and *D. simulans* (the best-studied species pair), it could be completed in 2 weeks. The sensitivity of the test could probably be increased by using three input frequencies so that the parameters of the DeWit competition model could be estimated. *While Drosophila competition may play an important role in the development of a theory of ecotoxicology, it does not appear to be sufficiently representative of important interactions in the field to warrant its use as a test protocol.*

(b) *Other flies*. Although the great preponderance of literature on competition between flies is concerned with *Drosophila*, significant work has been done on other species. These include species of blowfly (Ullyett 1950), housefly and blowfly (Pimentel, Feinberg et al. 1965), and varieties of housefly (Boggild and Keiding

1958; Sokal and Sullivan 1963). In addition to being less well studied than *Drosophila*, these species require more space and therefore would be more expensive to maintain. *Therefore, they are not recommended*.

(c) *Tribolium*. Competition between flour beetles of the genus *Tribolium* has been studied at least as much as *Drosophila* competition. More than 100 papers have been published on *Tribolium* competition since Park's (1948) seminal monograph. These studies have been concerned with the ways in which competition leads to extinction of one or the other member of the pair *T. confusum* (cf) and *T. castaneum* (cs). The characteristic of this system that has attracted the most attention is the indeterminacy of outcome. At certain initial frequencies of specified populations and at specified temperatures and humidity, the surviving species cannot be predicted. This indeterminacy indicates a fine competitive balance. Therefore, *Tribolium* competition, like *Drosophila* competition, may be highly sensitive to a wide range of chemicals.

The *Tribolium* system is easily initiated by placing the desired proportions of the two species in shell vials containing 8 g of whole wheat flour with 5% yeast. All life stages are removed by sieving at monthly intervals and placing in fresh medium. A tentative testing protocol proposed for this system calls for operating the system under conditions that produce an indeterminant outcome (Suter 1980a). The primary response criterion proposed is determinacy of outcome. That is, an effect has been demonstrated if one species becomes extinct in all chemically treated replicates. Time to extinction would be a secondary response criterion. The difficulty with this proposal is that the indeterminate systems require about 2 years for completion. This large time requirement results from the longevity of the adult beetles [323 days for cf and 213 for cs (Mertz 1972)] and their relatively long generation time (30 days). If, as was conjectured in the proposed protocol, the determinacy of the outcome could be predicted with 90% accuracy after 150 days, the system is still not as rapid as other screening tests. A single generation test for *Tribolium* competition would require a month, and there is no basis for predicting outcome from the results of a single generation as there is for *Drosophila*.

Because these species exist almost entirely as pests of stored grain products, the laboratory system is the "natural" system. The outcome of competition in these "natural" systems is, however, immaterial to the grain products owner. *The particular combination of exploitation competition with predation and cannibalism that characterizes this system is unlikely to respond in a manner that is predictive of interaction in any important group of organisms.*

(d) *Other grain insects*. Park was preceded in the study of competition among grain insects by Crombie (1945, 1946), who studied the beetles *T. confusum*, *Rhizopertha dominica*, and *Oryzaephilus* *surinamensis* and the moth *Sitotroga cerealella*. These studies, like those of Park, were initiated to investigate problems in population biology. Crombie's systems were supplanted by Park's because of the greater theoretical appeal of competition between sibling species. More recently, LeCato (1975a, 1975b, and 1978) reexamined systems of taxonomically diverse graminivorous insects with the idea of reducing grain losses by encouraging predation. If this idea ever proves useful (the research has been at least temporarily discontinued), the effects of fumigants and residues of pesticides or other chemicals in the grain would be critical.

(e) *Soil arthropods*. Detritivorous soil and litter arthropods show a remarkable combination of high species diversity and low feeding specificity (Anderson 1962). This "enigma" gives the problem of soil arthropod competition theoretical importance. These organisms can be maintained as competitors on a totally artificial system of plaster of Paris and charcoal (Culver 1974; Longstaff 1976) or in soil-litter microcosms (Anderson 1978). The former system is too artificial to represent effects of chemicals in the field and is too poorly understood and developed to be appealing as a screening test. On the other hand, microarthropods in soil and litter are relatively difficult to extract quantitatively and census. These organisms are important primarily because of their collaborative role in decomposition and nutrient cycling. Tests for these processes are discussed in Sect. 4.2.

(4) *Other animals*. *No competition tests are recommended for competition among nonarthropod animals*. Nematodes approach the arthropods in ecological importance, but they are difficult to identify and are therefore poor candidates for a population test. Vertebrates are obviously important, but testing for effects on competition between populations of even the smallest species (as opposed to simple behavioral interactions) would require an excessively large area and long time period.

4.1.2 Herbivore-Plant

This section considers herbivorous insects feeding on flowering plants. These two groups dominate the earth's biota, accounting for more than 60% of procaryotic species (Gilbert 1979). Insects account for the great preponderance of herbivory, rivaled only by ungulates in semiarid grasslands. Ungulate herbivory, for obvious reasons, is not considered for laboratory test systems.

While herbivores may act as predators (by killing individual plants) or as overtly mutualistic symbionts, most herbivores are functionally analogous to parasites, consuming the tissues or fluids of the host plant without directly killing it (Gilbert 1979). It has been hypothesized that consumption of plant parts by herbivores generally increases the overall fitness of the host plants (Owen and Wiegert 1976); the success of programs to control exotic weeds by importing herbivorous insects from the weed's area of origin suggests that such cryptomutualism is not the rule. Certainly, intensive agricultural and sylvicultural practices tend to uncouple such mutualistic relationships, resulting in highly "virulent" herbivores. Nevertheless, the fact that herbivorous insects can modify the allocation of plant resources in ways that are not always detrimental (Harris 1973) suggests that net plant production must be measured by tissue type and age to understand herbivore effects.

Herbivores that feed on vegetation can be divided into chewing and sucking types. Sucking insects have several advantages as test organisms: (1) they are typically small, and many of them can be crowded on a single plant; (2) many of them are either immobile or relatively inactive except during dispersal phases; (3) they are highly sensitive to changes in plant physiology as reflected in sap chemistry; (4) many of them produce several generations per year; and (5) most economically important species have several known predators that may be added to the system (Sect. 4.1.3). While these insects may be highly sensitive to chemicals that are taken up by the plant (witness the efficiency of systemic pesticides), they would be insensitive to chemicals deposited on the leaf surface. For such chemicals, an external chewing insect test system would be required.

Because of the relatively long life cycles of flowering plants, herbivore-plant population interaction tests would probably be limited to growing the plant through seed set. Even with this reduction in scope, there are no apparent existing laboratory systems for this interaction (effects of herbivory over one full life cycle of the plant). Population ecologists have avoided the problems of maintaining live plants by using insects that can be raised on inert media (e.g., *Drosophila* and *Tribolium*). Agricultural and ecosystem entomologists typically raise insects on stems or individual leaves of plants when determining consumption rates or pesticide response. Whole-plant cages (Adams and Van Emden 1972) are seldom used, in part because of effects of the cage on light, humidity, and other environmental conditions. Large (>0.5 m^2) cages that contain several potted plants probably provide better conditions, but if each plant is to be treated as a replicate, nonflying insects must be used, and mobile forms such as apterous aphids must be constrained by barriers (Adams and Van Emden 1972). Because the great majority of studies of plant-herbivore interactions are conducted in the field, there is little experience with these laboratory systems. Test systems would need to be largely developed from scratch, but there do not appear to be major technical problems.

The life cycles of many herbivorous insects are sufficiently long and complex that most insects and the plants could not practically be raised through multiple life cycles in routine tests. Indicator tests that only include the activities of certain life stages might be developed for those population interactions. These tests must be chosen to include stages in development that are likely to be sensitive to a variety of chemicals (ecdysis may be an example) and those stages that are sensitive to the resistance mechanisms of the host plants. Antibiotic plant defensive mechanisms act at various stages in the life cycle of the insect to inhibit growth, reduce survival, disrupt development, or reduce reproduction (Waiss et al. 1977). Test chemicals may reduce or enhance host plant resistance.

This section emphasizes herbivores using domestic plants because (1) these species are well known, (2) the plants are easily cultivated, (3) many of the insects can be obtained from culture (Dickerson et al. 1980) and maintained on defined artificial diets, and (4) their social relevance is obvious. Highly coevolved herbivore-plant species pairs from natural communities may, however, prove to be more sensitive and more representative of the majority of the earth's biota. This possibility should be considered during development of advanced test systems.

(1) Sucking Insect-Plant. While some hemipterans are important herbivores, the majority of sucking herbivorous insects are homopterans. As previously mentioned, these insects have several advantages as test organisms. The herbivore-plant species pairs discussed in this section were selected primarily on the basis of a recent workshop held at ORNL (Suter 1981a).

(a) Aphid-alfalfa. The spotted alfalfa aphid (Therioaphis trifolli) is an important pest of alfalfa in California and other western states. It is a good candidate for a test system to represent this class of interactions because it involves an economically important host plant that can be easily and rapidly grown. The system could be readily extended to include predators [Sect. 4.1.3(2)], and it might be possible to create an aphid competition test by adding the pea aphid (Acyrthosiphon pisum), which is also a pest of alfalfa in California. While no suitable experimental or testing system has been demonstrated for these species, it should be relatively easy to adapt the techniques of mass rearing aphids on potted alfalfa seedlings (Finney et al. 1960) to testing by using whole-plant cages.

(b) Aphid-grain. Individual, whole-plant cages were used by Windle and Franz (1979) in a study of the effects of greenbugs (Schizaphis graminum) on competition between barley varieties. Greenbugs, a chronic pest of small grains, caused a reversal in competitive dominance as measured by the crowding coefficient [Sect. 4.1.1(2)] in aphid-resistant and susceptible varieties. Effects of aphids on plant production were demonstrated within 2 weeks, but the effect changed from positive to negative between weeks 2 and 6.

(c) Whitefly-plant. The greenhouse whitefly (Trialeurodes vaporariorum) is an important pest of greenhouse crops with over 200 host plants. The relevance of this system to greenhouse culture is both its chief advantage and its chief disadvantage. The test and real world conditions are identical, but whiteflies are insignificant in the United States outside of greenhouses and citrus groves. The greenhouse whitefly can be raised on potted beans, cotton, tomatoes, or any of its many other host plants. It has a generation time of 21 days at 20°C, which includes a crawler stage of the first instar, scale-like second and third instars, a "pupa" and winged adult. Although whole greenhouses have been used as experimental units in whitefly control studies, a test system would use whole-plant cages (Nechols and Tauber 1977).

(d) *Scale-plant*. Scale insects (Coccoidea) present considerable advantages for determining life table data because of their sessile nature and the record of mortality provided by the shells. The brown soft scale (*Coccus hesperidum*) uses citrus and other tropical and subtropical trees and a large variety of greenhouse plants. Its development may be completed in 26 days at 27°C, and the primarily parthenogenic females may produce over 200 progeny (Saakyan-Baranova 1964). This scale is easily maintained in the laboratory on *Coleus* or *Begonia*.

(2) *Chewing insect-plant*. Chewing herbivores, primarily Coleoptera, Lepidoptera, and Orthoptera, are ecologically and economically important and represent a distinct mode of plant-insect-chemical interaction. Most of them are difficult to maintain in the laboratory over multiple generations because the adults are relatively large and highly mobile and have different requirements from the larvae. Because many of them are also voracious, they would require relatively large plants to moderate herbivory to a level at which plant responses could be measured.

No clearly preferable insect-plant species pair for this test system exists. A recent workshop recommended that tests for chewing herbivore-plant interactions should utilize the corn earworm (cotton bollworm, tomato fruit worm, *Heliothis zea*) and possibly the corn rootworm, japanese beetle, *Cactoblastis*, gypsy moth, and a grasshopper because they are well studied, economically important, and have documented exploiters (Suter 1981a). The corn earworm could be easily cultured because it is hearty and euryphagous, but it is fairly large and is probably insensitive to pesticides and other chemicals. Some other species such as the gypsy moth and *Cactoblastis* are relatively unsuitable because they use slowly growing hosts. The alfalfa caterpillar (*Colias eurytheme*) and green cloverworm (*Plathypena scabra*) are somewhat smaller important species which consume alfalfa, an easily and rapidly grown herb.

The fact that the young and the adults share the same habitat gives grasshoppers and other orthoptera an advantage over lepidoptera. Some beetles, such as the Mexican bean beetle (*Epilachna varivestis*), share this advantage even though they are homometabolous and small.

The physical test system for this relationship in most cases must be some sort of whole-plant cage. Dyer and Bokhari (1976) maintained individual grasshoppers (*Melanoplus sanguinipes*) for 18 days in single plant cages containing hydroponic blue grama grass (*Bouteloua gracilis*). Larger cages containing several plants will be required for true studies of population interactions. Soil-dwelling herbivores such as the corn rootworm can be maintained in pots or even in plastic pouches (Ortman and Branson 1976). Nonflying insects may be isolated by placing a sticky trap around each plant (Robinson et al. 1978). This technique provides a measure of emigration which could indicate a change in herbivore preference.

4.1.3 Predator-Prey

Predation is often defined functionally as all forms of exploitation that regularly result in death of the exploited species. That definition is used here except for herbivory because herbivory is predominately nonlethal. The definition includes parasitoids and microbial "parasites" such as *Bdellovibrio*, but not pathogens and true parasites, which typically do not kill or consume a large fraction of an individual host.

Predator effectiveness is the product of the predation rate and the population growth rate of the herbivore and behavioral response to predation. Predation rates are the product of changes in predator density (numerical responses) and the predation rate per individual (functional responses) (Solomon 1949). Most laboratory studies of terrestrial predation are concerned with the components of the functional response, searching rate, capture rate, handling time, and satiation. Numerical responses are relatively neglected because of the difficulty of maintaining predators and prey together in the laboratory for multiple generations. Prey species are typically presented to the predator under circumstances that do not permit an appropriate behavioral response by the prey; they very seldom reproduce in the experimental system, and they may even be replaced by artificial prey (e.g., Holling 1966; Gardner 1966).

(1) *Microbe-microbe*. While most studies of microbes that kill and consume other microbes are concerned with protozoan predators, the predatory habit is also practiced by a variety of bacteria and fungi. Microbial predation may be considered beneficial if the prey is a plant pathogen (e.g., Habte and Alexander 1975) or detrimental if it is a beneficial species such as *Rhizobium* (e.g., Danso et al. 1975).

Because of the relative difficulty of quantitatively extracting and enumerating microbes in soil, it is recommended that any tests involving enumeration of microbial predators and prey be conducted in aquatic systems. Predation on plant pathogens can be evaluated in terms of the presence of plant pathology. The best example of this type of system is the control of *Rhizoctonia solani* through destruction of its sclerotia by *Tricoderma harzisnum*. *A test protocol* for this system using damping-off of radishes as the measured response has been tentatively proposed (Suter 1981a). Respiration and transformation of mineral nutrients by prey organisms have also been used as indicators of the effects of microbial predators (e.g., Telegdy-Kovats 1932). These responses are discussed as ecosystem processes [Sect. 4.2.5 (4)].

(2) Arthropod-predators. Traditionally defined predators kill their prey before consuming them or kill them by consuming them rather rapidly. Parasitoids differ in that they kill their host (prey) by consuming them over a relatively long time. It has been argued on theoretical grounds that parasitoids are better adapted than most other predators to control the populations of herbivorous insects (Doutt and DeBach 1964). This argument is borne out by the predominance of parasitoids in successful insect biocontrol programs. Therefore, parasitoids are emphasized in this section.

The relatively high sensitivity of arthropod predators to pesticides suggests that they may provide sensitive toxicological tests. Pesticide applications commonly eliminate arthropod predators, often resulting in the creation of secondary pests and the resurgence of primary pests to greater abundance than before treatment. The effectiveness of a predator as a biocontrol agent can be verified in the field by applying pesticides at concentrations that eliminate the predator without damaging the prey populations (DeBach and Huffaker 1971). The effectiveness of predation may be even more sensitive than predator mortality.

Laboratory studies of predators as potential biocontrol agents generally are not concerned with the population biology of the predator and prey species. Population interactions are studied in the field. Laboratory studies of the relative toxicity of pesticides to predators and prey generally measure mortality rather than effects on the predation process. Therefore, laboratory test systems for arthropod predator-prey population interactions cannot readily be adapted from existing experimental systems for biocontrol agents. As a rule, ecological experiments use easily manipulated, interesting, or unusual species (Sects. (a), (e), and (f) below) rather than important species.

Searching capacity has been found to be the most important indicator of the ability of predators in biocontrol programs to maintain pest populations below an economic threshold (Huffaker et al. 1971). Therefore, some basis for using predation rate as an indicator of predator-prey population interactions exists. Nevertheless, tests that only use predation rate or its components should be supported by studies of true population interactions.

(a) Parasitoid-gall midge. The California endemic midge Rhopalomyia californica (Cecidomyiidae) that forms galls on Baccharis pilularis is attacked by 12 species of hymenopteran parasitoids.

Force (1970, 1974) has performed field and laboratory investigations of this "community" to elucidate the means by which this diversity of parasitoids is maintained and its effect on the midge. The community experiments are performed in 48- by 38- by 40-cm screened cages with 40 *Bacharis* seedlings in small pots. The cages are kept in a greenhouse. The midge and the six parasitoid species used in these experiments are not available from culture, but they are readily obtained by collecting galls and are easily maintained in the laboratory. The life cycles of three parasitoids investigated are 27, 38, and 46 days.

Six species of parasitoids can be maintained together in a cage for at least 100 days. The outcome is determined by details of the biology of the parasitoids, including restraint from and success in superparasitism, multiparasitism, and hyperparasitism. This system is particularly well developed for studying population interactions between parasitoid competitors and between parasitoids and their host. It does not represent an economically important species association, and none of the biological constituents are commercially available. The physical system of large, whole-plant cages could serve as a model for test systems using other species.

(b) *Parasitoid-whitefly*. Since the 1920s the parasitoid *Encarsia formosa* has been used as a biocontrol agent for the greenhouse whitefly (Helgesen and Tauber 1974). At 18°C the fecundity of the whitefly is 10 times as great as that of *Encarsia* although the rate of development is equal; at 26°C the fecundity is equal, and the rate of development of the parasitoid is twice that of the whitefly (Hussey and Bravenboer 1971). *Encarsia* attacks the scale larvae of the whitefly, and parasitized scales are blackened and therefore readily recognized. *Encarsia* completes its life cycle in 2 to 4 weeks. This species pair is well studied; its dynamics in the greenhouse are relatively predictable (Burnett 1967), and the parasitoid is commercially available.

(c) *Parasitoid-aphid*. Three parasitoids of the spotted alfalfa aphid, *Praon exsoletum* (*P. palitans*), *Trioxys complanatus* (*T. utilis*), and *Aphelinus asychis* (*A. semiflavus*), have been the subjects of intensive laboratory study. Force and Messenger's (1964a and b, 1965) system of alfalfa stem "bouquets" in 3.5- by 15-cm glass tubes was designed to study the effects of physical conditions on the life history parameters of the parasitoids and on larval parasitoid competition. This system permits examination of parasitoid development and hunting efficiency of the adults although searching is minimized by the small chambers. *A larger system with whole plants would permit examination of true population interactions and would permit studies of searching*. Chemicals might affect the outcome of competition resulting from multiple parasitism, or they might diminish the ability of *A. asychis* to discriminate parasitized hosts.

(d) *Predator-aphid*. The best-studied predators of aphids are coccinellid (ladybird) beetles. Populations of the spotted alfalfa aphid are reduced by native coccinellid predators of the genera *Hyspodamia* and *Coccinella*. These predators have been the subject of considerable field investigation (Hagen, van den Bosch, and Dahlsten 1971) and would contribute to the completeness of a test system based on alfalfa and the spotted alfalfa aphid.

Laboratory studies of predation by coccinellids on aphids have been conducted using *C. septempunctata* on *Acyrithasiphon pisum* and *Aphis fabae* (Murdoch and Marks 1973) and *Adalia bipunctata* on *Drepanosiphon platanoides* (Dixon 1970), but these studies do not include full life cycles. Several species of coccinellids are commercially available.

Other aphid predators that could be used in a test system include green lacewings (*Chrysopa*), syrphid flies (*Syrphus*, *Metasyrphus*, etc.), and damsel bugs (*Nabis*). These predators are not as well studied or as readily available as coccinellids.

(e) *Parasitoid-grain moth*. Species of Lepidoptera from five families infest stored grains, pulses, nuts, and their products (Benson 1973). They are attacked by parasitoids from five families of Hymenoptera and one species of Diptera. Because of the economic importance of grain insects and their ease of manipulation in the laboratory, they have been the subjects of many laboratory studies.

Parasitoid-grain moth experimental systems consist of sets of replicate chambers, ranging in size from 0.005 to 13.8 m^3. Several containers of grain or other substrate are placed in the chambers with moths and parasitoids. The life cycles of a typical moth *Ephesta* (*Anagasta*) *kuhniella* and parasitoid *Exidechthis canescens* are 41 to 106 days and 21 to 33 days, respectively, at 27°C. The system could be elaborated by incorporating multiple prey and parasitoid species or the oophagous mite *Blattisocius*.

Because the parasitoids discover prey by probing the substrate with the ovipositers, searching efficiency is the key factor in the parasitoid population even in small (0.61-m^3) chambers (Benson 1973). By providing refuges for the moth larvae, the system can be made to persist for 2 years or more in 0.13-m^3 chambers (Flanders and Badgley 1963). Thus, the system lends itself to tests of both predation rate and true population interactions. This system has considerable advantages because of extensive previous laboratory study and ease of manipulation resulting from the use of grain rather than whole plants to support the herbivore. The chief disadvantage of the system is that it is only directly relevant to grain storage. While the mechanisms of parasitoid-host interaction may be sufficiently uniform to permit generalization from this system, chemically treated grain would not be directly analagous to any important mode of ecosystem contamination.

(f) *Parasitoid-bean weevil*. Another set of important and rather extensive laboratory studies of predation are those conducted by Syunro Utida on the parasitoids of the azuki bean weevil (*Callosobruchus chinensis*) (summarized in Utida 1957). Bean weevils were raised on azuki beans in petri dishes and exposed to the braconid parasitoid *Heterospilus prosopidis*, alone or in competition with the chalcid parasitoid, *Neocatolaccus namezophagus*. To study population fluctuations, Utida counted the populations at 7- to 10-day intervals and ran the experiments for several months. Generation time for the bean weevils is three weeks. *As a potential test system, this experimental system shares the advantages and disadvantages of the parasitoid grain moth system already described*. While the azuki bean weevil is not readily available in the United States, a similar system has recently been developed utilizing another bean weevil (*Zabrotes subfasciatus*) with the parasitoids *H. prosopidis* and *Anisopteromalus calandrae* (Kistler 1980).

(g) *Parasitoid-fly*. This system was developed by David Pimentel to investigate the mechanisms of predator-prey coexistence. The system consists of an array of 1, 16, or 30 plastic boxes connected by plastic tubes (Pimentel et al. 1963). The boxes contain vials of medium on which houseflies (*Musca domestica*), blowflies (*Phaenicia sericata*), bluebottle flies (*Phormia regina*), or greenbottle flies (*Phaenicia sericata*) are raised. These serve as prey for the hymenopteran parasitoid *Nasonia vitripennis*. The predation rate of another fly pupa parasitoid (*Muscidifurax raptor*) has been studied relative to *N. vitripennis* (DeBach and Smith 1941) and could be used as a competitor in this system. The housefly, blowfly, and *Nasonia* have life cycles of 13, 14, and 14 days respectively. These three species are commercially available.

This system is similar to the parasitoid-grain moth system because its population ecology is relatively well known, and it is based on a medium that is convenient, but not directly relevant to field conditions. Searching efficiency of the parasitoid is not an important factor in the system as constituted so it is not useful for tests on predation rate. This system emphasizes the coevolution of fecundity of the parasitoid and resistance of the fly. It would be difficult, however, to demonstrate that coevolution was reduced by a chemical.

Such a system could be developed using *Drosophila* and the parasitoid *Pseudeucoila bochei*. Use of these species should allow some miniaturization of the system. In addition, there has been far more experience with *Drosophila* than with houseflies or blowflies.

(h) *Ground-dwelling beetle-prey*. Staphylinid and carabid beetles are common predators of ground-dwelling arthropods and molluscs. While these beetles have been shown in the field to be important predators of a variety of insect pests, few laboratory studies have been performed on them.

Harris and Oliver (1979) examined predation by the staphylinid Philonthus creunatus on the eggs and larvae of the hornfly Haematobia irritans. Hornfly eggs were placed on manure pats, which were placed on either a soil-vermiculite mixture or a section of sod. Beetles were added in varying densities, and the emerging flies were counted. While this system appears to realistically simulate the field situation, it was sustained for less than a full generation of either the predator or prey. Because the beetles primarily consume the egg stage of the fly, behavior of the prey is not an important component of the system, and chemical exposure of the prey should begin before the predation test.

Small carabids such as Notiophilus can consume collembola in simple arenas (Eijsackers 1978). Because collembola can be raised on plaster, charcoal, and yeast, a test of predation behavior could be easily developed. A population test would require soil for the immature carabids, which would considerably complicate enumeration of both prey and predator.

Because neither of these systems for predator-prey interactions using ground-dwelling beetles appears promising, development is not recommended. It should be possible to introduce these predators into Pimentel's fly system [Sects. 4.1.1(3) and 4.1.3(2)] to test the generality of the responses observed.

(i) Spider-prey. Although spiders are major predators in many natural ecosystems, interest in their role as predators has been limited because they have not been shown to control outbreaks of insect pests. Laboratory studies of spider predation have been concerned with spider behavior; those that study the functional response to prey density most closely approximate a population interaction test (Haynes and Sisojevic 1966; Gardner 1966; Hardman and Turnbull 1974). Drosophila, which were used as prey in these studies, are easily obtained and cultured, but spiders are not commercially available, and techniques for rearing spiders are only now being developed.

(j) Mite-mite. Unlike insect predators and prey, herbivorous and predatory mites have been well studied as interacting populations in realistic laboratory conditions (Table 4.1). This is probably due, in large part, to Huffaker and Kennett's (1956) demonstration that the dynamics of mite predatory-prey interactions in strawberry fields are adequately simulated by laboratory studies. Most of these experimental systems consist of mites on arrays of potted plants in a greenhouse or environmental chamber, with water or grease barriers used to isolate treatments or individual plants within treatments. Although the mites are counted in sample leaves or plants, the outcome is typically described in terms of control (the herbivore population reaches levels that damage the plant). The control of a herbivore by a predator depends not only on the pair of species used but also on physical conditions, the characteristics of the host plant, and the input ratio of the predator and prey. Systems

TABLE 4.1. LABORATORY STUDIES OF MITE-MITE PREDATION

Study	Predator	Prey	Host
Huffaker and Kennett 1956	*Typhlodromus cucumeris* *T. reticulatus*	*Tarsonemus pallidus*	Strawberry
Huffaker 1958, Huffaker et al. 1963	*Typhlodromus occidentalis*	*Eotetranychus sexmaxulatus*	Oranges
Collyer 1958	*Typhlodromus tiliae*	*Panonychus ulmi*	*Prunus* sp.
Chant 1961	*Phytoseiulus persimilis*	*Tetranychus telarius*	Red kidney bean
Herbert 1962	*Typhlodromus pyri*	*Bryobia arboria*	Apple
Van de Vrie 1962	*Typhlodromus tiliae* *T. tiliarum*	*Panonychus ulmi*	Apple
Collyer 1964	*Typhlodromus pyri* *T. finlandicus*	*Aculus fockeui* *Panonychus ulmi*	Bullace
Hussey et al. 1965	*Phytoseiglus riegeli*	*Tetranychus urticae*	Cucumber
McMurtry and Scriven 1968	*Amblyseius hibisci*	*Oligonychus punicae*	Avocado
Burnett 1970	*Amblyseius fallacis*	*Tetranychus urticae*	Alfalfa

that are near the balance point between control and escape of the prey might be highly sensitive to chemical perturbations. The test might be scored on the basis of the presence or absence of large numbers of mites. For most of the systems listed in Table 4.1, this outcome would be reached in less than a month.

Huffaker's system of predator and prey mites on oranges (Huffaker et al. 1963) had considerable heuristic value in the development of ecology. This system is, however, much more difficult to relate to the real world than a system on plants, and its elaborate array of 252 partially covered oranges was difficult to establish and maintain.

(3) *Vertebrate predators*. Holling's (1959) laboratory studies of the functional response of deer mice (*Peromyscus maniculatus*) hunting pine sawfly (*Neodiprion sertifler*) cocoons were important to the development of the theory of predation. Similar studies of predatory behavior in enclosed arenas have since been conducted using a variety of other vertebrates (e.g., Craig 1978). This type of system is not a good candidate for protocol development because relatively large arenas are required (3 by 1.2 by 1.8 m in Holling's case), population responses are not included, and behavioral effects of chemicals on vertebrates are already being tested in relation to human health effects.

4.1.4 Host-Parasite

The experimental determination of effects of chemicals on host-parasite interaction has been treated as a rather complex, single-species problem. In one view, the parasite is considered as a second stress that, like thermal shock, modifies the intensity of the host's response to the chemical. Alternatively, chemicals are treated as potential drugs that may rid the host of the parasite. In neither case are the host and parasite treated as a system of interacting populations. This situation partly reflects a general lack of interest by experimental ecologists in parasitism relative to other types of population interactions as a result of the apparent absence of an experimentally tractable conceptual scale. The appropriate scale for laboratory population experiments lies somewhere between the microscale of medical physiology, described above, and the macroscale at which epidemiologists model or monitor the spread of infection and the evolution of virulence and resistance.

Even if a laboratory host-parasite population system were found or developed, it would not necessarily be a good test system. Because host-parasite relations are highly intimate and coevolved, their dynamics are dominated by peculiarities of structure and physiology that are not readily generalized.

For these reasons, host-parasite population interactions are not considered further in this document. Parasites of insects and plants that might be developed as traditional tests for effects on virulence are discussed in the report of a recent ORNL workshop (Suter 1981a).

4.1.5 Symbiosis

Symbiotic relationships are defined as those which benefit at least one of the partner species without harming either; these include Odum's (1971) commensalism, mutualism, and protocooperation. Because of the great diversity of ways in which one species may benefit another, the mechanisms of symbiosis are probably less uniform than those of most other classes of population interactions. They range from very intimate obligate relationships such as the termite-intestinal flagellate relationship to the rather loose commensal relationships such as phoresy.

This section deals primarily with the symbiotic relationships between higher plants and mycorrhizal and nitrogen-fixing microorganisms. Because these relationships are ubiquitous and important to primary production, they have the broadest relevance and greatest ecological and social importance of any symbiotic relationship. Lichens are considerably less important, but are obvious candidates for a testing protocol because of their use in air pollution monitoring.

(1) Lichens. Although many of the algal and fungal symbionts that form lichens are capable of independent existence, the symbiotic unit is functionally and reproductively distinct from its constituents. The existence of an independent taxonomic nomenclature for lichens reflects the proto-organismal character of lichens. Because lichen tests are performed by collecting whole lichens rather than by bringing together the constituent symbionts (a difficult and seldom successful procedure), lichen tests are procedurally identical to single-species tests. Therefore, it can be argued that lichens do not constitute a multispecies test system.

Lichens are highly sensitive to gaseous air pollutants, particularly SO_2 (Ferry et al. 1973). They may also be sensitive to organic vapors and aerosols. Lichen tests are performed by exposing a piece of thallus that has been activated by wetting to the chemical vapor or aerosol. Potential response parameters include respiration, photosynthesis growth, pigmentation, potassium loss, and death.

(2) Rhizobium-legume. Although nitrogen fixation is carried out by a variety of free-living microbes and microbes living symbiotically with higher plants (Alexander 1971), the Rhizobium-legume symbiosis is the predominate source of fixed nitrogen in terrestrial ecosystems. Because of the agricultural importance of legumes, numerous tests have been conducted to determine the effects of agricultural chemicals on Rhizobium-legume symbiosis. Because the sensitivity of in vitro rhizobia is poorly correlated with sensitivity of the whole plant-microbe system (Lin et al. 1972, Fisher 1976, and Fisher et al.

1978), only whole-system tests should be considered. Rhizobia-inoculated seeds or sprouts can be grown on agar slants or in soil or artificial media (vermiculite, sand, etc.). The growth medium can significantly influence response to a chemical. Because simple media such as vermiculite may decrease rather than increase the sensitivity of the test without reducing variability (Smith et al. 1978), soil should be used as the growth medium for the sake of realism.

The ultimate socially relevant response of this system is productivity of the legume partner. Parameters that may be measured include weight of plant parts, number and weight of propagules, frequency of flowering, stem elongation, and damage symptoms. Nitrogen content of plant parts provides an integrative measure of nitrogen fixation and is also an indicator of forage quality. Direct indicators of the symbiotic relationship include the number, position, size, and color of nodules; leghaemoglobin content; and nitrogen fixation rate of the whole system or of excised roots or nodules. None of these parameters are clearly more sensitive to toxicants than the others (Table 4.2), and most are easily determined. The N fixation rate and plant N content determinations require some analytic sophistication, but at least one of these parameters should be determined as an indication of the effectiveness of the nodules.

The few time-course studies shown in Table 5.2 indicate that sensitivity of the system generally diminishes with time. This may be simply explained by degradation of the test chemical and adaptation of the symbionts, or it may be the result of reduction in sensitivity of the symbiont pair with age. Letchworth and Blum (1977) found that sensitivity of clover top weight and number of nodules to ozone decreased with the age at which the plants were exposed. Nodulation of the first root (crown nodules) is more variable than nodulation of lateral roots (Tu 1977) and thus may be more sensitive to toxicants. *Therefore, a short-term test using legume seedlings may be sensitive and may indicate the potential for interference problems with establishment and reproduction of legumes*. A more realistic test for pasture legumes and natural legumes would be provided by the fescue-clover competition system discussed in Sect. 4.1.1(2), but this system is less well developed.

(3) *Mycorrhizae*. Most flowering plants form mycorrhizal associations with fungi. The primary benefit ascribed to mycorrhizae is enhanced uptake of phosphorus. Mycorrhizae may also enhance uptake of other nutrients and water and protect the plant from root diseases. While the mycorrhizal association is generally beneficial to the higher symbiont, under certain environmental conditions, mycorrhizae may be neutral or even parasitic. Chemicals may not only deprive plants of the benefits of mycorrhizal symbiosis, but may modify the symbiotic nature of the association.

The benefits of this association can be measured directly in terms of the quantity and quality of plant production. The

TABLE 4.2. RELATIVE FREQUENCY OF SIGNIFICANT RESPONSES BY PARAMETERS OF THE RHIZOBIUM-LEGUME SYMBIOSIS TO TOXIC CHEMICALS

Study	Legume weight			Damage	Seed production	Flowering	Stem elongation	N content of the legume	Total nodules	Nodule size	Leghaemoglobin content	% infection	N fixation
	Top	Roots	Total										
Pareek and Gaur 1970 DDT	$0/6^a$ $(28)^b$ $4/6^-$ (49)				0/6 (28) $1/6^+$ $3/6^-$ (49)			$2/6^+$ $3/6^-$ (28) $5/6^-$ (49)	$1/6^+$ $2/6^-$ (28) $2/6^+$ $4/6^-$ (49)		$3/6^+$ $3/6^-$ (28) $3/6^+$ $3/6^-$ (49)		
Selim et al. 1970 Dieldrin and Lindane	$2/4^-$ (60)	$2/4^-$ (60)	$2/4^-$ (60)			$4/4^-$ (60)	$1/4^-$ (60)	$2/4^-$ (60)	$4/4^-$ (60)	$2/4^-$ (60)			
Carlyle and Thorpe 1947 2-4, D (Na and NH_3 salts)				$15/24^+$ (134)					$23/24^-$ (34)				
Letchworth and Blum 1977: O_3	$2/2^-$ (7-28)	$2/2^-$ (7-28)						$2/2^-$ (7-28)	$2/2^-$ (7-28)			0/2 (7-28)	
Grossbard 1970: 4 herbicides			$1/6^+$	0/6				$1/6^+$				$2/6^-$	
Tu 1978 3 insectides and 4 combinations	$4/7^-$ (21) 0/7 (56)	$5/7^-$ (21) 0/7 (56)							$4/7^-$ (21) 0/7 (56)				$6/7^-$ (21) 0/7 (56)

TABLE 4.2 (continued)

Study	Legume weight			Damage	Seed production	Flowering	Stem elongation	N content of the legume	Total nodules	Nodule size	Leghaemoglobin content	% infection	N fixation
	Top	Roots	Total										
Fisher et al. 1978 8 surfactant fungicides	12/15$^-$ (56) 3/15$^-$ (84)												8/15$^-$ (56) 4/15$^-$ (84)
Maning, Feder and Papia 1972: O_3	1/1$^-$ (20) 1/1 (60)	1/1$^-$ (20) 1/1 (60)			1/1$^-$ (20) 1/1 (60)		1/1$^-$ (20) 1/1 (60)		1/1$^-$ (20) 1/1 (60)	1/1$^-$ (20) 1/1 (60)			
Fisher 1976: 8 fungicides			0/16 (77)					0/16 (77)			0/14 (77)		1/14$^+$ 2/14$^-$ (77)
Smith et al. 1978 7 pesticides				26/112$^+$ (21)									61/112$^-$ (21)
Kulkarni et al. 1974 4 insectides				0/4 (56)		0/4 (56)		0/4 (56)	4/4$^-$ (56)	0/4 (56)	0/4 (56)		

[a] The fraction indicates the number of significant responses out of the total number of combinations of toxicants and soils. The sign (+ or -) indicates that the parameter increased or decreased.

[b] Numbers in parentheses indicate the number of days after addition of the chemicals that responses were measured.

mycorrhizal association itself can be examined according to the extent of infection. Ectomycorrhizal infection can be readily evaluated in terms of the amount of root covered with a mycelial mantle. Endomycorrhizae do not significantly modify the appearance of infected roots and therefore must be evaluated microscopically. Preparation techniques have been developed by Ambler and Young (1977) and Kormanik et al. (1980). These techniques are used to measure percent infection and the frequency of arbuscules and vesicules. These measures of infection are likely to respond more rapidly than plant production to a chemical that affects the association and may be more sensitive than plant production. The large clamydospores of endomycorrhizae are readily removed by wet sieving, but clamydospore production is less sensitive than root infection to pesticides (Menge et al. 1979). Of 39 combinations of crops and pesticides, 24 resulted in reduced endomycorrhizal infection (Menge et al. 1979).

It may also be possible to develop a test system based on the ability of mycorrhizae to suppress root diseases. Mycorrhizae may inhibit pathogens (1) by producing antibiotics, (2) by stimulating the root to produce antibiotics, (3) by modifying root exudates, or (4) by forming a physical barrier to infection (Marx 1969). A root disease that produced a rapid visible response and that was suppressed by mycorrhizae would form an easily scored and possibly sensitive test system.

Because of the taxonomic, functional, and structural differences between endomycorrhizae and ectomycorrhizae, test systems should be developed for both types of associations. The difference in sensitivity between the two types is unknown, but endomycorrhizae recover more slowly because they do not form airborne spores. Tentative protocols for *Pisolithus tinctorius* and loblolly pine (ectomycorrhizae) and *Glomus* spp. and a grass (endomycorrhizae) have been proposed by participants in a recent workshop at ORNL (Suter 1981a). These protocols call for rather long test runs (105 and 84 days), but it may be possible to distinguish effects of chemicals on infection rates more rapidly. Any test system that includes a plant can serve as a test for the mycorrhizal association if suitable inoculum is included. Any phytotoxicity test that uses nonmycorrhizal plants is likely to give results that are irrelevant to field conditions.

4.1.6 Community Composition

The properties that are unique to the community level of organization include species composition, succession, food web structure, species turnover rate, and diversity. Multicellular plants and macroinvertebrate and vertebrate animals are too large and long-lived to display these properties in the laboratory. Microbes and microinvertebrates, as previously mentioned, are difficult to extract quantitatively, identify, and enumerate. Because the soil community's composition is not sufficiently important relative to its function to justify a difficult and expensive test, no tests for terrestrial community properties are recommended.

4.1.7 Summary

While terrestrial ecosystem-level responses to chemicals have received some attention (Sect. 4.2), population interactions have been neglected. The only interactions that have received significant toxicological attention and therefore could be adopted in the near term as TSCA test standards are the legume-rhizobia and mycorrhizal fungus-plant associations. Development is needed to arrive at acceptable protocols for these symbiotic associations because there has been no consistency in the techniques used to date. The test systems suggested in a recent ORNL workshop (Suter 1981a) would be a good starting point. In addition, the opinions expressed at that workshop and in Sect. 4.1.5 concerning appropriate response parameters must be confirmed by systematic testing with reference chemicals. The economic and ecological importance of these plant-microbe associations makes development of these tests highly desirable.

Drosophila and Tribolium competition, Pimentel's fly and wasp systems, and the parasitoid-grain moth system constitute a second class of potential test systems. These are highly developed experimental systems, which could be readily implemented but for which there is no toxicological experience. These systems may be quite sensitive, but their ability to generate relevant predictions is questionable. Because these systems are relatively well understood and fairly easily operated, they might be examined concurrently with the developing test protocols to better understand the way in which chemicals affect general classes of population interactions.

Finally, there is a group of potential test systems that is neither well studied toxicologically nor well developed as experimental systems, but that appears worthy of long-term development. This category includes general interactions: plant competition, herbivory, and predation. The best candidate for a plant competition test is clover-grass because of its economic importance, its seminatural character, and the work done on its response to ozone. No strong bases for selecting a particular species of host plant and a sucking or chewing insect for herbivory tests exist. For the reasons listed in Sect. 4.1.2, small homoptera appear to be good subjects for a population interaction test. Hymenopteran parasitoids are the best candidates for the predators in a predator-prey test because they are small, important as biocontrol agents, and well studied. While the parasitoid-grain moth and fly systems are relatively well studied and easily maintained, a system involving parasitoids of homoptera raised on whole plants should be much more representative of natural and agronomic systems. A similarly realistic test for conventional predators would include a coccinellid or neuropteran predator and a homopteran prey raised on whole plants. Mite predator-prey systems are relatively well developed, compact, and rapid. They would be ideal test systems if they can be shown to be representative of insects as well as mites.

The potential for combining categories of tests is obvious. One can easily imagine, for example, a test system involving competition between clover and grass that is inoculated with *Rhizobium* and mycorrhizae and that supports competing herbivores and predators. Such a system would have considerable appeal as a highly inclusive and realistic screening test, but simpler systems would be necessary to explain the cause of the observed responses.

The use of any of these tests for broad predictions of ecological effects will depend on a considerable increase in our knowledge of the nature of ecological processes. Some bases for that knowledge will result from the process of test development.

4.2 Ecosystem Properties

The two basic processes which are characteristic of ecosystems are the cycling of nutrient elements and the capture and transfer of energy. While chemical contaminants may modify the physical and chemical components of these processes by affecting soil pH or by chelating metal ions, TSCA chemicals are unlikely to occur in the environment at concentrations sufficient to have significant direct effects on soil chemistry unless large spills occur. Effects on the terrestrial biota are likely to be far more significant.

This section discusses the parameters measured in tests for effects on nutrient dynamics, primary production, and saprophytic metabolism in terrestrial ecosystems. Nonsaprophytic secondary production is not considered because it is much less readily measured as a whole ecosystem characteristic than as a component of specific population interactions (Sect. 4.1). Problems of selecting the size and components of test systems are also discussed. Examples of synthetic and excised test systems are briefly described in terms of their relative applicability to toxicological testing.

4.2.1 Parameters

(1) Primary productivity. The ecological importance and social relevance of certain ecosystem processes are evident. For example, the ecologist's primary production is the forester's and agriculturalist's yield. This parameter might be a sufficient test criterion in itself, except that response to chemicals may be very slow because of the mediation by effects on soil chemistry, reproductive success, herbivore and pathogen activity, or other factors. Hazard evaluation procedures involving any system that contains plants should include primary production, measured in terms of dry mass yield because of its importance and ease of determination. Transient effects on primary production from which the plant recovers can be detected by CO_2 uptake or O_2 release, but if these effects are

not reflected in yield, their importance is questionable. Other, easily measured plant characteristics that may aid in the interpretation of test results include (a) symptoms of damage such as chlorosis and necrosis, (b) phenological parameters such as time to flowering, and (c) physiological parameters such as the nutrient status of the leaves.

(2) Nutrient cycling. Processes that influence soil fertility (nutrient cycling processes), such as transformations and movement of nutrient elements and degradation of organic materials, also have obvious social relevance. Nutrient transformations include fixation, mineralization, and oxidation-reduction reactions. The most important transformations in terms of biological production are those that involve the macronutrients. Of these, the best candidates for toxicological testing are nitrogen and sulfur, the macronutrients whose dynamics are dominated by biological processes. (Carbon dynamics are considered in terms of photosynthesis and respiration.) Nitrogen is the most important, but not all steps in the N cycle are important in all systems. Nitrogen fixation makes an insignificant contribution in most agricultural systems because of fertilization (fixation by legumes is an exception) and in mature natural systems because of the dominance of internal cycling. Nitrogen is often important in natural pastures and immature natural ecosystems, and nitrogen mineralization (ammonification) is important in natural systems. Nitrification is considered undesirable in many agricultural systems because of nitrate leaching and is a minor process in many natural systems because of rapid immobilization of ammonia. Biological nitrogen immobilization is important in nearly all systems, but it is difficult to measure directly; indirect indicators include plant N content and available N concentrations. Denitrification is limited under aerobic conditions, and inhibition of this process would generally not be considered detrimental.

Loss of nutrient elements by leaching can be important to ecosystem maintenance and productivity if sufficiently large and sustained. It has also been hypothesized to be a rapid and highly sensitive indicator of ecosystem stress (O'Neill et al. 1977). The terrestrial portion of a recent microcosm research program at ORNL was based on this premise (Harris 1980). The synthesis of this effort concluded that Ca and NO_3 leaching would be sufficient parameters for use in a toxicology screening test (Ross-Todd et al. 1980). Ca concentrations in leachate had the least variance and the greatest sensitivity of the nutrients considered [Mg, Ca, dissolved organic carbon (DOC), K, NO_3, P, and NH_4] followed by Mg, which was highly correlated with Ca. NO_3 loss was much more variable than Ca and Mg, but was highly sensitive.

The mechanisms of nutrient loss in these test systems, particularly Ca loss, are not understood. The large importance of cation exchange processes and carbonate chemistry relative to biological processes in most soils raises important questions of interpretation. When Jackson et al. (1979) used Na_2SO_4 as a nontoxic control salt for Na_3AsO_4, Ca leaching was higher in the controls than in the experimentals. Van Voris et al. (1978) added ^{45}Ca to the surface of a Cd-contaminated grassland core. They concluded that "the Ca isotope was totally retained in the top 2.5 cm of the soil indicating that the Ca loss was not due to cation exchange since the ion exchange sites were not saturated." The results can be realistically explained by isotopic dilution, the process of displacement of native Ca on exchange sites by ^{45}Ca; the experiment, therefore, did not eliminate exchange processes as a major factor in Ca loss. The coincidental occurrence of increased Ca loss and decreased CO_2 efflux cited by Van Voris et al. (1978) is suggestive, but it does not establish a biological cause for Ca loss.

Nutrient export becomes even more difficult to interpret when organic chemicals are tested. Metabolism of an organic chemical leads to immobilization of nutrients, masking any leakage of nutrients from stressed biota. This process might explain why hexachlorobenzene caused greater Ca loss at lower concentrations in a soil core study by Ausmus et al. (1979). Gile et al. (1979) examined the effects of four organic agricultural chemicals on nutrient loss. Leaching of most nutrients was unaffected or reduced by the chemicals, again suggesting that immobilization was stimulated. Because most TSCA test substances will be organic, this could be a serious disadvantage to using nutrient export tests to predict effects.

Other problems with nutrient leaching studies concern interpretation of results in terms of effects in the field. Leaching of nutrients from a 5- to 15-cm-deep soil core does not mean that the nutrients will appear in surface or ground water or that they are lost to the biotic community. In many, if not most cases, nutrients leached from the A horizon are retained in lower soil horizons. In this case the nutrient is not lost, but rather has been mobilized and transferred to another relatively immobile pool. This movement would be advantageous to deeper-rooted plant species. A second problem is the inability to adequately interpret the seriousness of the observed response. In soil microcosms, a toxicant-elevated nutrient loss rate typically returns to control levels within 3 weeks, even though toxicant and nutrient concentrations in the soil have not appreciably declined. A parameter that is that resilient will only be useful if it is indicative of longer-term ecosystem responses.

Another approach to determining the effect of chemicals on nutrient dynamics is to measure nutrient availability by extraction. Such extractions are conventionally performed by shaking a soil slurry formed with dried, screened soil and a chemical extractant. Jackson and Hall (1978) leached soil cores with extractant solutions, thereby deriving estimates of available Ca, NH_3, NO_3, and PO_4 that were lower than those obtained from slurries, but that were more sensitive to the effects of heavy metals. Like nutrient leaching, nutrient availability would respond to effects on mineralization and immobilization. It has the advantage over nutrient leaching of explicitly taking into account ion exchange processes, but its response is less often significant, and the direction of response is less regular (Ausmus et al. 1979; Jackson et al. 1979; and Jackson et al. 1978).

(3) Community metabolism. The most common measure of soil metabolism is CO_2 efflux. Chemicals that are toxic and persistent and to which the biota cannot adapt will simply depress CO_2 efflux. Chemicals that serve as substrates or supply mineral nutrients would elevate CO_2 efflux. Chemicals that are toxic but leave no residues such as fumigants, that are readily degraded, or to which the biota adapts cause a short depression in CO_2 efflux, followed by a rebound to very high levels and a slower return to predisturbance levels. This pattern also occurs in response to drying or physical disturbance of the soil, in which case the cycle typically requires 5 to 14 days. It is one of the major determinants of the equilibration period required for soil test systems. Elevated CO_2 efflux during the rebound period is generally attributed to the degradation of microbes killed by the disturbance.

If CO_2 efflux is measured continuously by infrared gas analysis, cycles in the system's carbon balance can be monitored. The number of distinguishable cyclic frequencies was used by Van Voris et al. (1978) as an indicator of the functional complexity of microcosms. This index, however, was used to predict response to a toxicant rather than as an indicator of response. The functional significance of these cycles is unknown.

Carbonaceous substrates are frequently added to the soil to examine effects of chemicals on a specific degradation process or to ease the CO_2 determination by increasing the efflux rate. In the absence of evidence that degradation of a specific substrate is particularly sensitive to toxic chemicals, it is probably best to maximize realism by using no amendment or by using only whole plant material. In this way, the range of microbes involved in the test is maximized. If, as Domsch (1970) has hypothesized, autochthonous organisms and those that degrade resistant substances are most sensitive to toxic effects, degradation of native soil organic matter may be a sensitive process. If carbonaceous amendments are used, the time until peak respiration may be more sensitive than total respiration (Domsch 1970; Spalding 1978).

Other methods of determining soil community metabolism include O_2 uptake, heat production, and ATP concentration. Methods of measuring O_2 consumption (a) are less precise and therefore less sensitive than CO_2 efflux (Lighthart et al. 1977), (b) do not represent microbial respiration as completely as CO_2 (Stotzky 1965), and (c) therefore would only be useful if the respiratory quotient (RQ) was of interest. Klein (1977) found that RQ was a sensitive indicator of seasonal changes in the microbial community, but it was not affected by any of the 14 salts of heavy metals that significantly reduced CO_2 efflux (Lighthart et al. 1977).

ATP assays are difficult and expensive to perform, are not amenable to time course analysis because of their destructive nature, and do not seem to offer any particular advantages over other indices of soil metabolism.

The sensitivity of soil metabolism to toxic chemicals is questionable. The only good body of evidence for disruption of decomposition by pollutants is that for heavy metals (Coughtrey et al. 1979; Harris 1980; Jackson and Watson 1977; Lighthart et al. 1977; Ruhling and Tyler 1973; Spalding 1978; Tyler 1976). This effect is generally attributed to metal toxicity. However, it has been attributed to total salt concentration by Lighthart et al. (1977) because sodium salts were as effective as heavy metal salts of equivalent ionic strength. Spalding (1978) concluded that the effect of heavy metals on soil respiration primarily resulted from the formation of resistant metal-organic complexes rather than from direct toxicity. These mechanisms would not contribute to the effects of organic compounds on decomposition. The effect of most organic compounds would be to increase metabolism by serving as a microbial substrate.

Enzyme activity determinations are used to indicate the potential of soils to perform certain chemical transformations. Results of enzyme assays reflect changes in the character of ecosystems less directly than the parameters previously discussed. Therefore, enzyme assays could only be recommended if they were known to be particularly sensitive to chemicals or particularly rapid and inexpensive. Because available evidence indicates that neither of these cases is true, enzyme assays are not recommended.

Transformation of chemical contaminants is also an ecosystem function. While this process typically results in detoxification, partial oxidation of chemicals can result in increased toxicity. One chemical may also decrease the rate of degradation of a second chemical, leading to undesired toxic effects and contamination of food or enhancing the effectiveness of agricultural chemicals that degrade too rapidly (Kaufman 1977). Effects of one pesticide on the degradation of another have been demonstrated by Kaufman et al. (1970, 1971, 1977). In addition to pesticides, the soil biota degrades toxic chemicals from the air, chemical spills, and buried or land-farmed wastes. The soil biota is also responsible for scavenging inorganic gaseous pollutants from the atmosphere. The extent and potential importance of interference with this process by chemicals is unknown.

(4) Summary. Table 4.3 summarizes the results of several studies that have examined the effects of toxic substances on more than one ecosystem process. Fungal and bacterial counts are included because they are frequently determined in studies of ecosystem processes. Few of these studies consider primary production, but the

results of one study suggest that it is more sensitive to organic chemicals than microbial processes and populations (Eno and Everett 1977) and should be determined in any system containing plants. CO_2 efflux is a rapid and sensitive indicator of biotic response, but it may increase or decrease depending on time since the perturbation, the degradability and persistence of the test chemical, the nutrient status of the system, and other factors. It should be measured over time to clarify the nature of the response. Mineralization of nitrogen and other nutrients is an important process that is relatively sensitive to metal salts (Liang and Tabatabi 1977) and moderately rapid. Nitrification and nitrogen fixation appear to be somewhat less sensitive and are as likely to increase as to decrease. The few results from ATP assays do not appear promising, particularly in light of the relatively high expense and difficulty of this assay. Enzyme assays, in addition to being difficult to interpret, appear to be relatively insensitive to perturbations. Nutrient leaching is sensitive to metal salts and is quite rapid in some cases, but to date the results with organic compounds are not promising. Nutrient availability appears to be less sensitive, consistent, and rapid than nutrient leaching.

There is good evidence that heavy metals disrupt ecosystem processes at concentrations that do not acutely affect most individual organisms. However, the studies cited herein and reviews of insecticide and herbicide effects on terrestrial ecosystems (Brown 1978; Greaves et al. 1976; Cullimore 1971) indicate that soil microbes and the ecosystem processes that they conduct are typically less sensitive to organic chemicals than individual organisms and populations. Because most TSCA-regulated chemicals are organic, they are more likely to behave like organic agrochemicals than metals. Nevertheless, effects on ecosystem processes are sufficiently important that a simple system to measure CO_2 efflux and N mineralization in soil should be included in any testing scheme. Other parameters such as nutrient leaching are potentially useful but require further development.

4.2.2 Test Components

While component ecosystem processes such as ammonification can be conducted by a single bacterial clone in a liquid minimum medium, the realism of responses measured in that system are highly questionable. Most microbial ecologists would agree that minimal realism requires a mixed microbial culture in soil. Some would argue further that because the presence of litter, plant roots, and soil invertebrates significantly modify the absolute and relative rates of soil processes, they must also be included in a test system for any basic ecosystem process. The importance of these components in determining responses to chemicals has not been investigated. CO_2 efflux has been measured in a wide variety of test systems, but its response shows no trends with increasing system complexity (Table 4.3). Nutrient leaching in response to metals is not clearly affected by the presence

TABLE 4.3. RELATIVE FREQUENCY OF SIGNIFICANT RESPONSES BY ECOSYSTEM PROCESS PARAMETERS TO TOXIC CHEMICALS IN LABORATORY SYSTEMS

							CO_2 efflux						
System (toxicant)	Primary production	Nutrient leaching	Nutrient availability	Nitrogen fixation	Ammonification	Nitrification	amended	Not amended	O_2 uptake	ATP	Enzyme assays	Bacteria counts	Fungal counts
SOIL													
Atlas, et al. 1978 (3 herbicides and 2 fungicides)				0/2[a] (84)[b]		0/6 (84)	1/8- (84)	0/6 (84)			2/4- (84)	0/6 (84)	1/5- (84)
Bartha et al. (29 pesticides)						3/29+ 22/29- (6-18)	7/17- (30)[d]	2/17- (30)[d]					
Eno and Everett 1958 (10 pesticides)	8/10- (17)					3/10+ 3/10- (30)		4/10+ (30)				0/10 (30)	1/10+ (30)
Kudeyarow and Jenkinson 1976 (CS_2 and $CHCl_3$)					4/4+ (10)	4/4- (10)		4/4+ (10)	4/4+ (10)				
Liang and Tabatabi 1977 (21 metal salts)					64/84- (20)	20/84- (20)							
Tu 1978 (32 pesticides)				7/32- 9/32+ 1/32± (2-6)								4/32- 7/32+ (2-6)	9/32- 5/32+ 3/32± (2-6)
Tu 1970 (4 pesticides)					7/8+ (7)	6/8- (2)			8/8+ [1]			1/8- [56] 1/8+ [28] 6/8± [7-56]	4/8- [7-56] 2/8+ [14-28] 1/8± [7-14]
Tu 1980 (7 pesticides)						0/14 (14) 4/14+ (28)			13/14+ [1]		11/24+ (2) 12/24+ (7) 16/24+ (14)	13/14- (7) 7/14- (14) 4/14+ (28)	12/14- (7) 6/14+ (14)
LITTER													
Spalding 1979 (7 metal salts)								6/7- (3-28)			5/63- 9/63+ (1-28)		
SOIL-LITTER													
Lighthart et al. 1977 (20 metal salts)								12/20- 1/20+ (20)	6/20- (20)				

TABLE 4.3. (continued)

System (toxicant)	Primary pro- duction	Nutrient leaching	Nutrient avail- ability	Nitrogen fixation	Ammoni- fication	Nitri- fication	CO_2 efflux		O_2 uptake	ATP	Enzyme assays	Bacteria counts	Fungal counts
							Amended	Not amended					
SOIL CORE													
Ausmus et al. 1979 (hexachlorobenzene)		1/1± [1][c]	0/1 (21)					1/1- (21)					
Gile et al. 1979 (Methyl parathion, dieldrin, 2, 4, 5-T and hexachlorobenzene)		2/20+ 5/20- (56)						0/1 (49)					
Jackson et al. 1977 (As)		2/4+ (?)								0/2 (?)	0/8 (?)		
GRASSLAND CORE													
Jackson et al. 1979 (As)	0/1 (107)	5/6+ 1/6- [1-107]	3/5+ (107)							0/1 (107)			1/1+ (107)
Van Voris et al. 1978 ($CdCl_2$)		1/1+ [1]						1/1- (14)		1/1- (62)		1/1+ (62)	1/1+ (62)
TREECOSM													
Jackson et al. 1978; Ausmus 1978 (Pb smelter dust)		4/5+ (611)	4/5- (611)					1/1+ [130]		1/1+ (611)		1/1+ (611)	1/1- (611)

[a] The fraction indicates the number of significant responses out of the total number of combinations of toxicants and soils. The sign indicates the direction of response; ± indicates that the direction changed over time.

[b] Numbers in parentheses indicate the number of days after addition of the toxicant that responses were measured.

[c] Numbers in brackets indicate the number of days in a time series of measurements when a significant response was first measured after addition of the toxicant.

[d] Total response for period indicated.

of plants although the treecosm responses may have been slowed by the trees and litter (Jackson et al. 1978). Extraneous components (those which do not qualitatively affect system response) would increase the cost of a test, would complicate interpretation of results, and might interfere with measurements. No ecosystem components have been shown to be extraneous in this sense.

Soil structure also can be considered a system component. Ausmus and O'Neill (1978) found that intact soil cores and homogenized soil columns did not differ in CO_2 efflux, but the homogenized soil lost significantly more DOC in leachate with a larger percent variation. In another study (Jackson et al. 1979; Jackson and Levine 1979) arsenic transport and nutrient concentrations in leachate before As treatment did not differ in 30-cm-diameter intact and homogenized soil columns; extractable Ca and PO_4 levels showed inconsistent differences. Leaching of DOC was higher in the intact columns (contradicting the result described above), and ATP concentration and fungal biomass were significantly reduced in the intact columns, but not in the homogenized columns. Although homogenized soil would seem intuitively to be less variable than intact cores, there were no consistent differences in variability in these studies. Therefore, the choice between intact and homogenized soil structures may be made on the basis of convenience. Small cores are most easily obtained by extraction, but larger systems such as the treecosm would probably be more easily assembled.

4.2.3 Soil Type

The problem of selecting a soil type for use in tests of terrestrial ecosystem processes is essentially the same as the problem of choosing species for tests of species interactions. The choice is critical to the outcome of the test because the responsiveness of ecosystem processes to chemicals is highly dependent on soil type.

One possible solution to the problem is to simply prescribe limits on soil texture, organic carbon content, and pH. This is the simplest solution and is probably the only one that is currently feasible, but unidentified discrepancies in results would still occur, and the range of field situations to which the test could apply would be limited. A second possible solution is to designate a standard soil or a series of standard soils that are representative of major regional soil types. This solution would produce relatively consistent results, but would require that EPA or some other agency be responsible for distributing certified standard soil. Another approach is to allow testing laboratories to select their test soil, but to require the use of standard reference chemicals as positive controls. This solution is based on the assumption that relative sensitivity of soils to different chemicals is nearly constant, at least within broad categories of chemicals and soils. This assumption will need to be tested before reference chemicals are proposed.

In some cases, the production, distribution, and use of a chemical may be so delimited as to allow identification of a small number of soils which could be affected by the chemical. In these cases, testing of the potentially affected soils would increase test validity at the cost of not producing standard results.

4.2.4 Size

The size of a test system is determined by (1) the components and processes that must be included, (2) the amount of material necessary for measurement of the response parameters, and (3) the necessity of reducing variance by increasing the volume of material. If plants or macroinvertebrates are included in the system, their requirements are likely to determine the minimum size. Laboratory systems are not large enough to support vertebrate animals without unrealistically severe disruption of the system (Gile and Gillett 1979; Metcalf et al. 1979). The volume of soil or litter in purely microbial systems is usually determined by the volumes required for chemical analysis or measurement of gas uptake or efflux.

Studies that consider the effect of size on system response are rare. Ross-Todd et al. (1980) analyzed the results of two experiments that considered the effect of size (10 x 10 cm vs 30 x 15 cm and 15 x 25 cm vs 30 x 25 cm) on response of grassland cores to As. The larger cores produced generally higher concentrations of nutrients in leachate, but the relative variability of this parameter was inconsistent. Leachate concentration showed a clearer treatment effect (was more sensitive) in the larger cores. CO_2 efflux was less variable in the larger cores. These results suggest that fewer large systems would be required to show a statistically significant treatment effect, but this advantage must be balanced against the higher cost of preparing and maintaining larger systems.

4.2.5 Synthetic Systems

This section discusses synthetic systems, those that are assembled or constructed from ecosystem components. The basic components are soil, plants, animals, and nonliving organic matter. The applicability of these systems to tilled fields where strong structural relationships of soil, litter, and plants do not develop is obvious. Natural ecosystems are probably less well simulated by these test systems than by excised, intact systems, but the differences in response have not been demonstrated in work to date.

Only one or a few key references are cited for each test system in this and the following section. A more complete set of references is provided in the bibliography (Appendix D).

(1) Soil systems. Most studies of terrestrial ecosystem processes are performed by microbiologists using natural microflora in soil. The soil may be dried, sieved, ground, formed into a slurry, or

amended with substrate materials. Slurries, like liquid cultures and agar plates, do not realistically represent the soil. Grinding is unnecessarily destructive, and sieving should be kept to a minimum to retain crumb structure. Drying is also unnecessary and reduces the diversity of the microflora. Soil amendments increase the rate and magnitude of microbial activities, making measurement easier, but they may qualitatively modify the effects of a test chemical if they are not representative of common substrates in the field. Glucose greatly decreases the sensitivity of microbial respiration to pesticides (Bartha 1967).

Soil systems (test systems consisting of soil and microbiota) can be used to test effects on any of the ecosystem processes previously discussed except those that require plants (primary production and plant uptake of nutrients). Decades of work by agronomic microbiologists indicate that nutrient dynamics and the effectiveness of soil fumigants in agricultural systems are adequately represented by soil systems. Untilled, natural systems may not be adequately represented by these systems because of the importance of litter-root-soil structure relationships.

Schemes for testing the effects of chemicals on soil processes have been suggested by Johnen and Drew (1977), Atlas et al. (1978), the U.S. EPA (1979), and the participants in a recent workshop held by ORNL (Suter 1981b). None of these schemes have been subject to validation, standardization, or interlaboratory transfer, but the test proposed at the ORNL workshop appears to best fit the requirements of TSCA.

(2) Litter. This system is identical to the soil system except that litter, rather than soil, is the medium (Spalding 1979). Litter responses to chemicals have received much less attention because forests have less economic importance than field crops and have received less intentional input of chemicals. Litter alone does not represent forest ecosystems as well as litter and soil and offers no significant advantage in cost or rapidity of response. Therefore, it does not appear to be a good candidate for protocol development.

(3) Soil-litter. This system is essentially a combination of the previous two, a layer of sifted litter on top of a layer of homogenized and sieved soil. In the form developed by Bond et al. (1976), the system is enclosed in an apparatus that permits continuous and simultaneous measurement of CO_2 efflux, O_2 uptake, and heat output. It is designed to make possible complete and accurate measurement of the integrated responses of the forest floor microbial community to toxicants. This system would be suitable for development as a test protocol if it was simplified by only measuring respiration as CO_2 efflux. Coefficients of variation for CO_2 efflux from this system are low (<10%) and comparable to those for intact forest soil cores (Ausmus and O'Neill 1978).

(4) Gnotobiotic soil. Rather than using a natural, undefined community of microflora and fauna in soil test systems, a defined community can be assembled in sterilized soil (Coleman et al. 1977). These gnotobiotic systems are useful research tools and are likely to be sensitive because they lack functional redundancy. However, they are expensive and difficult to maintain and are unlikely to respond as realistically to test chemicals as natural soil communities. For these reasons, gnotobiotic systems are not good candidates for test protocols.

(5) Soil-plant. These systems are designed to reveal the effect or fate of agricultural chemicals applied to field crops.

(a) Pot. This is essentially a test for effects of pesticides on crop plants using a pot of field soil in which effects on the microbial community and microbial processes are determined (Eno and Everett 1958). The use of large pots makes it possible to grow the plants to maturity and examine effects on reproduction and yield. The simplicity of this system and the large mass of experience with growing potted plants in greenhouses makes this an appealing test system for effects of chemicals on agricultural systems.

(b) Lichtenstein. This system consists of corn seedlings grown in layers of contaminated and uncontaminated homogenized soil contained in an 86- by 154-mm-high plastic cylinder, resting in a leachate collector (Lichtenstein et al. 1977). The only validation provided for this system is comparison of the results for a pesticide (N-2596) with an independent field study. In that study, far shorter persistence was found in the soil of field plots planted to rye than was found in the Lichtenstein system (Lichtenstein et al. 1977). This system is also essentially a pot test, except that the pots are not large enough to grow the plants to maturity.

(c) Agroecosystem chamber. This system consists of crop plants (cotton or tomatoes at five plants/chamber) grown on a 15-cm layer of sieved soil in a 115 cm high x 150 cm x 50 cm closed glass box with controlled air flow (Nash et al. 1977). The system is designed to provide a complete description of pesticide fate by permitting the measurement of volatilization and residues in soil, plants, and leachate. No attempts to field validate this system have been reported. The chief advantage of this system for effects studies is that the air flow system would permit measurement of whole system respiration.

(d) Summary. As effects tests, these systems are essentially plants in different-sized pots, one of which has a cover to control air flow. This type of system could be adapted to measure nutrient leaching in agricultural ecosystems, and microbial processes can be measured if the potting medium is not artificial. With the deliberate addition of a pathogen, herbivore, or another plant, a more realistic ecosystem process test and a test for population interactions are presumably obtained. The primary technical problem concerns the size of pot that is necessary to support the processes of interest.

(6) Soil, litter, plant, and animal. These systems represent attempts to assemble true microcosms--laboratory systems that contain all the major components and processes of a selected terrestrial ecosystem.

(a) Odum. This system consists of natural soil and litter and small plants of five different taxa in a 16.2-cm-diameter plastic desiccator (Odum and Lugo 1970). An air flow of 2.5 L/min was maintained through ports in the lid, and CO_2 content was measured with an infrared gas analyzer. Because the soil and litter were not subjected to harsh treatments and the flora consisted of whole transplants, a representative invertebrate fauna was included.

The purpose of this system was to supplement a field study of radiation effects on a tropical forest. The system permitted greater resolution in metabolic measurements than did the unconfined ecosystem. Neither respiration nor photosynthesis was found to be affected in these systems by 25,000 r of gamma radiation. The lack of effects on respiration was not surprising because respiration is dominated by the microflora, which are resistant to radiation. The absence of effects on photosynthesis was somewhat unexpected because damage to plants outside the microcosms was observed at that radiation level, but the photosynthetic enzyme system is resistant to radiation at levels that cause morphological damage to plants. The baseline respiration rate was two orders of magnitude lower in the microcosms than in the field.

(b) Witkamp. These systems were designed as research tools to study the dynamics of fallout isotopes (^{137}Cs) and mineral nutrients under various physical and biological conditions (Witkamp 1976). They consist of a glass or plastic cylinder 7 to 13 cm in diameter by 10 to 13 cm deep, with a leachate port to which various combinations of soil, litter, soil fauna, and seedling trees may be added. They have not been used for chemical testing, but have the advantage that their nutrient dynamics have been modeled and are relatively well understood. The approach of using major system elements as components in a factorial design would be useful for determining mechanisms of toxic response. Transfer rates are generally higher in these systems than in the field, but the mechanisms and pathways are qualitatively similar (Witkamp 1976).

(c) Metcalf. The original version of this system consisted of sloping soil in an aquarium with a crop and terrestrial fauna on the high end and water and aquatic flora and fauna on the low end (Metcalf et al. 1971). More recently, this system has been supplanted by a more efficient design. It consists of either 400 g of vermiculite or 3000 g of soil planted with corn (Metcalf et al. 1979).

After 10 days, saltmarsh caterpillars, slugs, earthworms, and pillbugs are added. On day 15 a vole is added, and on day 20 the system is terminated. The primary purpose of this system is to analyze the fate of pesticides in agricultural systems. Effects are determined incidentally by measuring plant growth and noting deaths of animals.

The only validation provided for this system is a general comparison of pesticide fate in the system and the field. Results agree "very closely" (Metcalf et al. 1979). If this system were adapted for use in effects testing, the vole should be deleted. The voles greatly disrupt the systems by burrowing and typically consume the entire flora and fauna of the system. This situation is obviously not typical of the role of voles in ecosystems, and the diet provided is probably no more realistic than commercially prepared food for laboratory mice. The use of screw-topped jars provides a cheap and easily closed system for gas analysis.

(d) Terrestrial microcosm chamber (TMC). The TMC is essentially an enlargement and elaboration of the Metcalf system. It consists of a 1 x 0.75 x 0.6 m glass box with ports for airflow, water addition as rain or a "spring," and a leachate port (Gile and Gillett 1979). It contains 20 cm of synthetic soil, alfalfa, rye grass, two species of nematodes, earthworms, enchaetraeid worms, two species of pillbugs, mealworms, crickets, snails, and a pregnant vole. Like the Metcalf system, it is used primarily to study the fate of pesticides and secondarily to determine effects.

The TMC results with Dieldrin were validated by comparison with published field and laboratory studies. While many results are comparable, others are not. The concentration of residues in the vole are more than an order of magnitude higher than would be expected from field studies. The problems of including a mammal in a microcosm are reduced but not eliminated in this larger system.

The advantages of this larger, elaborate system over the Metcalf system have largely to do with studies of fate. If the vole is deleted, the Metcalf system has no significant relative disadvantages as a test system and is considerably cheaper and easier to operate.

4.2.6 Excised Systems

Systems that are excised, intact from the field, are discussed in this section. These systems were developed out of the belief that the structural relationships of soil, litter, and plants are critical to ecosystem dynamics.

(1) Soil core. A 5-cm-diameter by 5- or 10-cm-deep soil core is encased in a heat-shrunk polyvinylchloride (PVC) sleeve and supported on a leachate collector. Aboveground vegetation may be removed or left in place. The system was designed to serve as a general-purpose

test system for determining the fate and effects of toxic materials. This is the only one of the six systems discussed at the 1977 Workshop on Terrestrial Microcosms for which a testing protocol was proposed (Gillett and Witt 1979; see also Harris 1980). No attempt has been made to field validate this specific system, but the nutrient leaching results have been related to the general body of evidence on nutrient loss summarized by O'Neill et al. (1977). This system, which was developed at ORNL, has been used at the Corvallis Environmental Research Laboratory to test pesticides and herbicides (Gile et al.). The Corvallis study did not obtain the same regular increase in nutrient leaching that was obtained at ORNL even though one common chemical (hexachlorobenzene) was used; it is not clear whether the disparity is due to differences in the soils used or other factors.

(2) Grassland core. This system consists of intact cores that are sufficiently large (15- to 30-cm diameter by 10 to 25 cm) to support a representative portion of a grassland community. The 15-cm diameter cores of Van Voris et al. (1978) supported averages of 14 individual plants of 6.3 species. The version of this system recommended by Harris (1980) is supported on a Plexiglass disk with central port and encased in a heat-shrunk PVC sleeve. This system was designed to test the fate and effects of chemicals in grassland communities. Jackson et al. (1979) attempted to validate this system in the field. While nutrient leaching and soil ATP levels in the cores were affected by As, no response was measured in the field. Because the cores were kept in the field and because untreated cores and plots were comparable, this result implies that enclosure increases the sensitivity of these parameters.

(3) Sod. This system consists of a 16-cm diameter by 7-cm deep section of sod contained in a closed 4-L Nalgene jar (Campbell 1973). Ports are provided in the lid for periodic measurement of CO_2 production by infrared gas analysis. This system was designed to display the response of grassland ecosystems to stress. It is similar to the grassland core, but has no provision for monitoring nutrient loss. It offers no particular advantage as a test system.

(4) Treecosm. This system consists of an intact 45- x 45- x 25-cm block of forest soil containing an approximately 2-m-tall red maple sapling and associated ground flora (Jackson et al. 1978). The primary purpose of this system was to investigate the ability of microcosms to simulate a specific field perturbation and elucidate the mechanisms of the observed field response.

Comparison of treecosm results with studies by Jackson and Watson (1977) of the effects of smelter emissions on Crooked Creek watershed partially validate the system. While the pattern of uptake of metals from the smelter dust was similar to that at Crooked Creek, differences in transfer rates were sufficient to prevent development of a predictive transport model of Crooked Creek watershed from the treecosm results (Luxmore and Begovich 1979). This disparity was attributed to the physical conditions of the greenhouse in which the treecosms were kept. While the treecosms were treated to simulate areas at Crooked Creek receiving high metal deposition rates, the small increase in macronutrient pools observed in treecosm litter better simulated areas that received intermediate levels of deposition. Low macronutrient levels were observed in tree tissues at Crooked Creek, but not in the treecosm. The increased leaching of macronutrients from treated treecosms suggests a mechanism for the decreased macronutrient levels in the soil at Crooked Creek. The elevated soil respiration rates and ATP concentrations observed in treated treecosms contrast sharply with the reduced respiration and elevated litter biomass observed at Crooked Creek. Reduced fungal lengths in treated treecosms correspond to the reduction in amino sugar concentrations observed at Crooked Creek.

The disparities between treecosm and field results may be attributed to the greenhouse environment or to differences in soil and biota between Crooked Creek, Missouri, and Oak Ridge, Tennessee, the source of the treecosms. It seems likely, however, that many of the disparities are attributable to the 20-month period of the treecosm experiment, which is relatively short in terms of forest dynamics. The high levels of internal nutrient cycling in trees buffer them against changes in soil chemistry. This characteristic also delays any soil responses that depend on changes in characteristics of the litter fall or root dynamics.

Because trees and their mycorrhizal symbionts dominate the dynamics of forest ecosystems, the treecosm is the minimum system that displays all the major forest ecosystem processes. Assembling such a large system from soil, litter, and a nursery tree would probably be easier than excising a large block of soil, but might increase the equilibration period and reduce realism. The size of the system could be reduced by using a seedling rather than a sapling tree, but the effects of this change are unknown. It would be highly desirable to establish that inexpensive and rapidly responding parameters such as nutrient leaching from soil cores are not only indicative of system stress, but are predictive of changes in forest production or other socially valued parameters. In the absence of such an ideal test, the treecosm should be developed as a confirmatory test for forest ecosystem responses to stress.

(5) Outcrops. This system consists of excised sections of small isolated communities that have developed in depressions on rock outcrops (McCormick and Platt 1962). The excised sections are arranged in a concrete trough, which is sloped to provide drainage. The major appeal of this system is that an entire, clearly defined, simple community is recreated. However, this community type is not sufficiently common to support harvesting for TSCA testing or to be considered an important community type. In addition, the peculiar hydrology of these systems makes them unrepresentative of most terrestrial

ecosystems. These considerations preclude the development of this system as a testing protocol.

4.2.7 Summary

There has been no consistent line of laboratory system (microcosm) development oriented toward ecosystem processes that would lead to a clearly useful test system for ecosystem processes. Most terrestrial microcosms have been developed to suit the needs of a specific research program rather than as generally applicable testing tools. In addition, most microcosm research has been concerned with the transport and fate of chemicals rather than with their effects. Therefore, only a simple ecosystem-level test system can be recommended for immediate use.

This system would consist of soil with and without a realistic organic amendment. Parameters measured would include CO_2 efflux, nitrogen mineralization, and nitrification. A system of this type (see Suter 1981b, for a proposed protocol) would be reasonably rapid and inexpensive while providing a realistic test of ecologically important and relatively well-understood processes of terrestrial ecosystems. Because of the considerable experience of microbial ecologists with this type of system, development would consist primarily of determining whether soil characteristics can be defined to give comparable results among different laboratories. This exercise should include the development of positive controls.

Considerably more development will be required before more complex microcosms can be used as test systems. Basic questions about microcosm design, optimum size, and the importance of components such as litter, plants, and animals remain unresolved. It is still not clear that microcosms display important responses to chemicals that are not apparent in or predictable from simpler plant, animal, and microbe toxicity tests. Parameters such as nutrient leaching rates and the frequency distribution of community CO_2 exchange must be better understood in terms of their mechanisms and responses to chemicals before they can be used in standardized predictive test systems.

Development of microcosms as test systems must proceed by an orderly consideration of component interactions. Physical and biological components (including the microflora) should be treated as elements in a factorial design. A few well-studied pesticides or other chemicals should be used as surrogates for TSCA-regulated chemicals to maximize the bases for validation and comparison with standard test systems. Such a program would provide a firm basis for support of test protocol.

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MATHEMATICAL MODELS USEFUL IN CHEMICAL HAZARD ASSESSMENT

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SECTION 5

MATHEMATICAL MODELS USEFUL IN CHEMICAL HAZARD ASSESSMENT

Mathematical models and laboratory test systems are similar in that both can be viewed, for the purpose of hazard assessment, as analogues of natural ecosystems. However, they are not interchangeable. Whereas laboratory systems are composed of real organisms, mathematical models consist solely of mathematical representations of organisms. Thus, models are more tenuously connected to reality than are laboratory systems. Many alternative models (in principle, an infinite number) of any real ecosystem are possible. Moreover, similar, and equally plausible, models of the same ecosystem can yield radically different predictions about the response of the system to chemical stress. The all-important subject of model validation has in the past received too little attention and is the single greatest limitation on the use of mathematical models in hazard assessment. According to Shugart and O'Neill (1979), model validation is the most important problem remaining in the field of ecological modeling. The limitless variety of models and modeling methods confers advantages as well as disadvantages. In comparison to laboratory test systems, mathematical models are extraordinarily versatile. The number and identity of components included in a model, the detail with which each component is modeled, and the method used to analyze the model can be tailored to the specific needs of each hazard assessment.

This section focuses on general types of models rather than on specific models. There are two reasons for this emphasis. First, the number of types of models is far smaller than the number of individual models. The various types of models differ in applicability and practicality to a greater extent than do different models within the same type. Moreover, describing the characteristics, advantages, and disadvantages of types of models provides insights that can facilitate the design and evaluation of future models. Second, different types of models are required for different purposes. Many ways exist in which models can be used to evaluate hazards, from initial screening of classes of substances for potential effects to site-specific evaluations of specific substances. Selecting the best models for any given assessment involves both technical and nontechnical decisions that can only be made by persons involved in that assessment.

Relatively little work has been done on developing and applying mathematical models to predict effects of toxic substances on multipopulation systems and ecosystems. Many existing ecosystem simulation models and environmental fate models could be modified for toxic effects prediction. In addition to relatively complex simulation models, broad classes of simpler, more generalized models and modeling methodologies appear to be potentially useful in toxic effects assessment. Many of these models are not useful for site-specific assessments, and their predictions are primarily qualitative rather than quantitative. However, where applicable (e.g., in preliminary screening), they can be much more rapidly and inexpensively applied than can detailed simulation models.

In addition to the types of models available, evaluation criteria are discussed in this section. These criteria are important because they are needed (1) for judging the usefulness of models proposed for chemical effects assessment, (2) for designing future models, and (3) for deciding how specific models can best be utilized. These criteria relate not only to the properties of the models, but also to the match between the capabilities of the models and the objectives of hazard evaluation schemes. Much of the information discussed in this section is the result of a workshop, Mathematical Models Useful in Toxicity Assessment, sponsored by ORNL and EPA (Barnthouse 1981).

5.1 Available Models and Modeling Methodologies

During the workshop on mathematical models, three general categories of potentially useful models were discussed:

1. Ecosystem simulation models.
2. Generalized multipopulation models.
3. Alternative methodologies.

This section contains brief descriptions of the types of models and methodologies included in each category and of the advantages and disadvantages of each type for predicting the effects of chemical substances.

5.1.1 Ecosystem Simulation Models

Of the various kinds of models that can be used to predict effects of chemical substances on multipopulation complexes and ecosystems, ecosystem simulation models are the best known and the only kind to have had significant practical applications to date. They incorporate far more detailed representations of abiotic and biotic processes than do the other models discussed here. The major advantage of this detail is that the physical and chemical processes that govern the fate of chemical substances in the environment and the biological processes that govern the effects of these substances on organisms can be more realistically modeled. However, the complexity necessitated by this detail makes these models comparatively difficult and expensive to use. They frequently require extensive modification to be implemented on a computing system other than the one for which they were designed. These models are difficult for persons other than the original developers to use, unless extensive documentation (which is rare) is available. Perhaps more important, large amounts of relatively costly data are required to calibrate ecosystem simulation models. Reference data sets that can be used to calibrate models and to verify predictions made by models will be required before ecosystem simulation models can be profitably used in risk assessments.

(1) Terrestrial simulation models. Local, regional, and even global-scale models have been developed to predict the transport and fate of anthropogenic materials in terrestrial ecosystems. The best developed of these are the local-scale cycling models that are used to predict doses to man resulting from radioisotope releases (Hoffman et al. 1977). Regional-scale models of DDT cycling and bioaccumulation have been used in legal proceedings related to DDT regulation (Harrison et al 1970). Global-scale models are now being developed to assess and predict changes in atmospheric CO_2 levels due to fossil fuel combustion (Emanuel et al. 1980). The local and regional models can be used to predict the transport and bioaccumulation of chemical substances, provided that sufficient information on the relevant chemical properties of the substances is available. A major disadvantage of all these models is that they assume that the modeled substance behaves like a tracer and has no effects on the modeled system. All would require substantial modification and validation to predict effects.

Nonlinear ecosystem simulation models such as the biome models developed under the auspices of the International Biological Program (IBP) (e.g., Innis 1972) can, at least in principle, be used to predict chemical effects. The most important limitation to their use is that unusually large quantities of data are required to calibrate them. Even when calibrated, independent data sets (not usually available) are required for validation, i.e., to show that they can accurately predict the effects of stress on ecosystems.

Forest succession models (e.g., Shugart and West 1977) are now being used to simulate the effects of SO_x and forest management practices on the structure and productivity of forests. These models require minor modifications to predict effects of chemical substances, and the predictions made (changes in timber yield) are socially relevant. Data requirements are less severe than for IBP-type models, but only soil compartments and vegetation are modeled. Although effects on animals of forest successional changes caused by chemical substances may be indirectly inferred from model predictions, they cannot be predicted directly.

Other succession models have been used to evaluate environmental impacts on naturally occurring forests. Botkin (1973, 1977) considered the effects of CO_2 enrichment on plant growth and subsequent effects on forest dynamics. McLaughlin et al. (1978) and West et al. (1980) conducted model experiments on chronic air pollution stress expressed as a change in growth rates of pollution-sensitive trees.

A review of forest succession models by Shugart and West (1980) concluded that forest succession models can provide a necessary adjunct to laboratory-based assessments of environmental effects and that models will become increasingly important tools for prediction if human activities alter environmental conditions on a global scale.

(2) Aquatic Simulation Models. Many models have been developed to simulate the transport and fate of materials in aquatic ecosystems (e.g., Smith et al. 1977; Mogenson and Jorgensen 1979; Fagerstrom and Asell 1973). Some of these were constructed specifically to predict the transport and fate of chemical substances such as pesticides, PCBs, and heavy metals. Like the corresponding terrestrial fate models, they cannot be used to predict the effects of chemical substances on ecosystems. They must be modified or coupled to a model that can predict effects.

Nonlinear ecosystem simulation models exist for most types of aquatic ecosystems (e.g., Park et al. 1975; Scavia et al. 1976; Steele and Frost 1977; Kremer and Nixon 1978). Many of these models are detailed enough so that effects of chemical substances on organismal physiology can be extrapolated to population and ecosystem effects. The lower trophic levels (phytoplankton and zooplankton) are generally modeled in the greatest detail, and success at validating model predictions has been greatest at these levels.

A few models are now being developed that incorporate both sufficient physical and chemical detail to predict the fate of substances and enough biological detail to predict effects (e.g., Falco and Mulkey 1976). None of these models has been applied to date.

5.1.2 Generalized Multipopulation Models

Ecosystem simulation models are intended to be realistic representations of particular ecosystem types. Modifying them to model a different ecosystem can be time-consuming and expensive. Alternatively, it is also possible to construct simple, highly generalized multipopulation models that can be rapidly and inexpensively tailored to fit any system of interacting populations, aquatic or terrestrial. Using this modeling strategy, no attempt is made to model every component of an ecosystem; only those processes believed to be critically important are modeled. Transport phenomena are not incorporated in these models. Thus, they can be used to predict the effects of chemical substances on systems, but not the fate of those substances. These models are not thought to be appropriate for detailed chemical- and site-specific hazard assessments. They can be used in the early stages of an assessment to rapidly explore the possible effects of toxic substances. Results of these preliminary studies can aid in determining whether a more detailed modeling effort is warranted.

These models can be classified into four groups. In order of increasing complexity, these are:

1. Functionally simple, not environmentally coupled (e.g., DeAngelis et al. 1975; Canale 1970; Levin 1974; Hassell and Comins 1976).
2. Functionally simple, environmentally coupled (e.g., Emanuel and Mulholland 1975).
3. Functionally complex, not environmentally coupled (e.g., Hsu et al. 1977; Travis et al. 1980).
4. Functionally complex, environmentally coupled (e.g., Craig et al. 1979; Eggers 1975; Anderson and Ursin 1977).

Within each category, models can be either spatially homogeneous or spatially complex and either age-dependent or not. Although many of the cited examples were developed with particular systems of populations in mind, the principles used can be applied to any system.

5.1.3 Alternative methodologies

In additon to ecosystem simulation models and generalized multipopulation models, several less familiar modeling methods appear to be potentially useful in hazard assessment. Two of these, loop analysis and time-averaging, are methods of analyzing the qualitative behavior of systems of coupled differential equations. They could be applied to many of the generalized multipopulation models discussed in the previous section. A third method, input-output analysis, is a method of econometric analysis that has been modified for use in ecology. In addition to these newly developed methods, the well-developed (but infrequently applied) theory of population genetics may be useful in predicting the evolutionary responses of populations exposed to chemical substances.

(1) Loop analysis. Loop analysis (Levins 1974; Lane and Levins 1977) can be used to analyze partially specified systems of equations (i.e., systems in which the patterns of interaction among the component variables are known, but parameter values and functional forms are not). The definitions of the variables are entirely arbitrary (e.g., they can be populations, aggregated groups of populations, life-stages, or even physiological rates). Loop analysis has been used in theoretical studies of eutrophication (Lane and Levins 1977), but has not been used to predict effects of chemical substances. It can be used to predict the response of a multipopulation system to an applied stress, to identify critical parameters that should be measured, and to identify system properties that enhance or reduce impacts.

(2) Time-averaging. Time-averaging (Levins 1979) was designed to be complementary to loop analysis. In loop analysis, the system being modeled is assumed to be at, or at least close to, equilibrium. If the natural system being modeled is in reality far from equilibrium, conclusions drawn from loop analysis may not be valid. In contrast, time-averaging assumes that the system is fluctuating and is not at equilibrium.

Like loop analysis, time-averaging can be applied to any system of interacting populations or aggregates of populations. However, instead of focusing on average population (or aggregate population) sizes as in loop analysis, time-averaging focuses on the variances and covariances of the population sizes. In theory, measurements of these variances and covariances, and changes in variances and covariances in response to inputs of chemical substances, may be used to distinguish populations that are directly affected by a chemical substance from those that are indirectly affected. This application of time-averaging may be especially useful in interpreting the results of microcosm experiments.

(3) Input-output analysis. Input-output analysis is an econometric method that has been adapted for use in ecology (Hannon 1973; Finn 1976; Lettenmaier and Richey 1978). It has been used to compare material cycling patterns in different ecosystems. The analysis can be applied either to whole ecosystems or to subsystems within ecosystems. It has been hypothesized that structure and cycling indices derived by using input-output analysis may be useful as indicators of environmental stress. In theory, input-output analysis can be used to predict changes in material flow patterns in response to stress, but further development and testing are required before it is known whether this is feasible in practice.

(4) Population genetics models. Population biologists have used a variety of models to study the evolution of populations and systems of interacting populations in response to changes in their environments (e.g., Kimura and Ohta 1971). All of these models relate rates of changes in gene or phenotype frequencies to selective pressure, heritability, and genetic variance within populations. They can be used to predict adaptive responses of species to toxic substances and to predict the effects of those responses on population size, location, behavior, and interactions with other species.

Although population genetics models have not been used to predict the effects of chemical substances on populations, they are potentially valuable for this purpose because populations in nature frequently evolve in response to exposure to chemical substances. Pesticide tolerance in insects and antibiotic resistance in pathogens are notorious examples. Practical applications would require experimental work to measure the genetic variances in tolerance within and between populations for species of interest and to estimate selection intensities in the field.

5.2 Criteria for Evaluating and Selecting Models

No existing models have been demonstrated to be useful for predicting the effects of toxic substances on ecosystems. Moreover, no single model or model type can fulfill all regulatory needs. For this reason, one task at the workshop on Mathematical Models Useful in Toxicity Assessment was development of criteria that could be used to evaluate the usefulness of existing models, modified versions of existing models, and new models. These criteria include not only the properties of the models themselves, but also the match between the capabilities (and deficiencies) of the models and the objectives of a hazard assessment scheme. The criteria selected are defined as follows:

1. The degree of modification required for handling toxic material inputs. Can toxic material inputs be modeled directly? Are the physical and chemical processes that govern the transport and fate of toxic materials included in the model? Are the biological processes directly affected by toxic materials included in the model?

2. Data requirements. Is the amount of data required for parameterizing the model consistent with the available resources (i.e., time and money)?

3. Generality. Can the model be used for only one geographic region or ecosystem type, or can it be easily applied to others?

4. Ease of validation. Has the model been validated against baseline data? Are the output variables (i.e., those that must be measured to test the model's predictions) easily measurable? Do modifications required for handling toxic materials invalidate the model? Can the model be tested with microcosm systems and with field data?

5. Social relevance. Is the model output relevant to regulatory needs?

6. Relevance to monitoring. Does the model suggest an environmental monitoring protocol? For example, does it suggest indicator variables that are easily measurable and that could be used as early warnings of environmental effects.

7. Spatial/temporal scales. Do the spatial and temporal scales of the model match the basic impact scale?

8. Ease of use. Is the model documentation comprehensible, consistent, and complete? Is the computer code readily available? How much modification is required to implement the code on a different computer system?

9. Acceptance by the scientific community, especially the ecological community. Is the model based on biological ideas and mathematical procedures accepted by most of the ecological community?

Figure 5.1 presents a scheme that could be used to identify specific models for use in such evaluations. The scheme uses aquatic ecosystem simulation models as examples, but it could apply equally to any type of model. It is exceedingly important to note that the choice of the best model(s) for any given hazard assessment involves a number of decisions that require active participation by the Office of Toxic Substances. These decisions include formulating the specific legal or social questions that the model will be expected to answer and specifying whether the purpose of the assessment is the screening of many substances for potential effects or the detailed evaluation of particular substances in connection with regulatory actions.

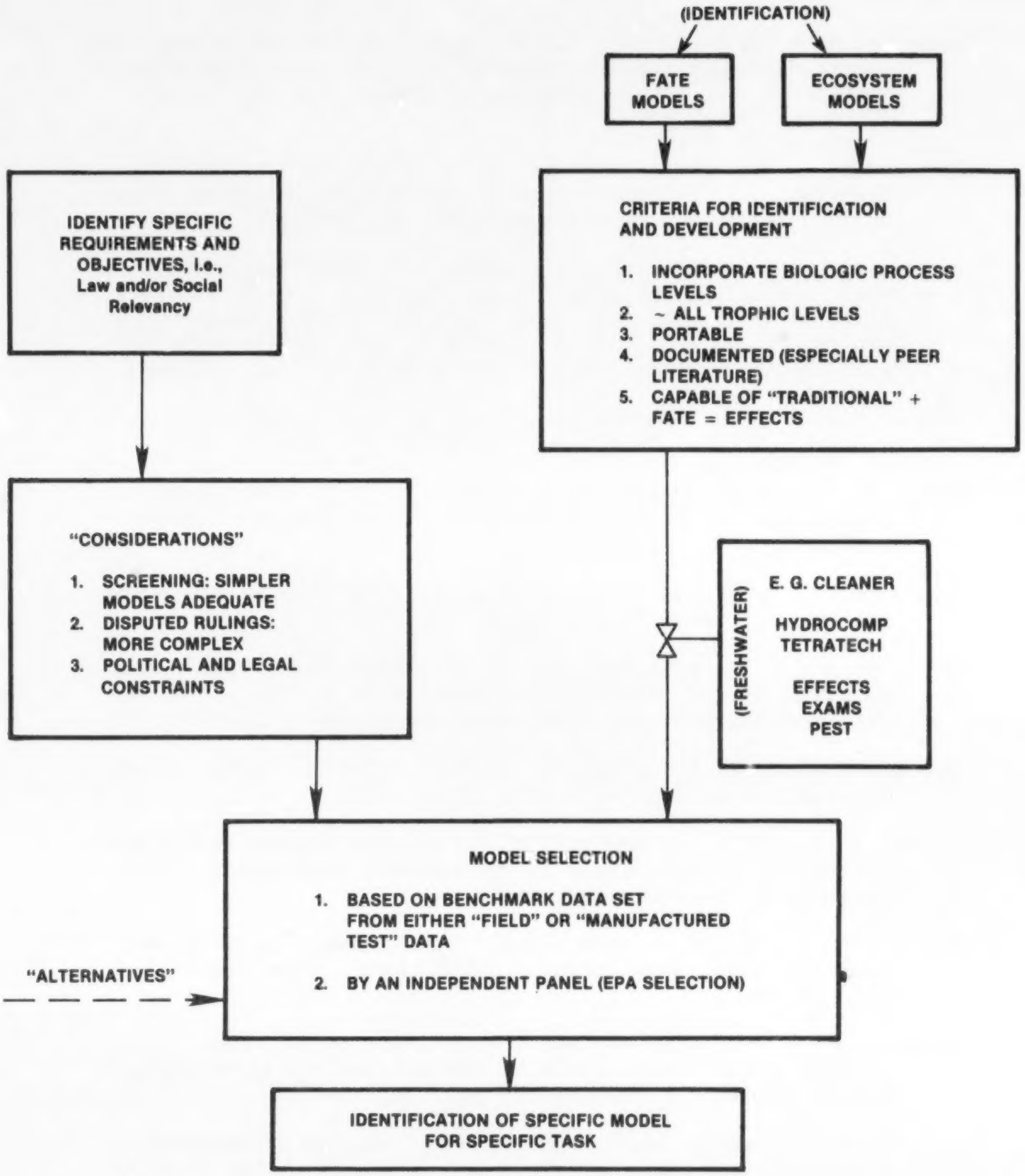
(IDENTIFICATION)
FATE MODELS
ECOSYSTEM MODELS
IDENTIFY SPECIFIC REQUIREMENTS AND OBJECTIVES, i.e., Law and/or Social Relevancy
CRITERIA FOR IDENTIFICATION AND DEVELOPMENT
1. INCORPORATE BIOLOGIC PROCESS LEVELS
2. ~ ALL TROPHIC LEVELS
3. PORTABLE
4. DOCUMENTED (ESPECIALLY PEER LITERATURE)
5. CAPABLE OF "TRADITIONAL" + FATE = EFFECTS
"CONSIDERATIONS"
1. SCREENING: SIMPLER MODELS ADEQUATE
2. DISPUTED RULINGS: MORE COMPLEX
3. POLITICAL AND LEGAL CONSTRAINTS
(FRESHWATER)
E. G. CLEANER
HYDROCOMP
TETRATECH
EFFECTS
EXAMS
PEST
MODEL SELECTION
1. BASED ON BENCHMARK DATA SET FROM EITHER "FIELD" OR "MANUFACTURED TEST" DATA
2. BY AN INDEPENDENT PANEL (EPA SELECTION)
"ALTERNATIVES"
IDENTIFICATION OF SPECIFIC MODEL FOR SPECIFIC TASK

FIGURE 5.1 SCHEME FOR SELECTING APPROPRIATE MODELS FOR USE IN HAZARD ASSESSMENTS.

5.3 References

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APPENDIX A*

SUMMARY TABLE OF AQUATIC TEST SYSTEMS

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*Complete references can be found in Section 3.7.

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APPENDIX A
SUMMARY TABLE OF AQUATIC TEST SYSTEMS

Author(s)	System components	Measured responses	Duration of expt.	Expt'l. variables	Validation
A. COMPETITION					
Fielding and Russell 1976	Algae (*Ectocarpus siliculosis*, *Ulothrix flacca*, *Erythrotrichia carnea*) in batch culture	Final yield (biomass)	35 days	Cu	
Fisher et al. 1974	Algae (*Dunaliella tertiolecta*, *Thalassiosira pseudonana*) in batch and continuous culture	Population density	7 to 16 days	PCB	
Frank 1957	*Daphnia magna*, *D. pulicaria*	Population density, size classes, sex ratios, # of ephippia, # of shed parthenogenic eggs	60 days	Food source	
Goulden and Horning 1980	*Daphnia galeata mendotae*, *Bosmina longirostris*	Population density, age classes, mortality	64 to 108 days		
Hansen and Hubbell 1980	Bacteria (*Escherichia coli*, *Pseudomonas aeruginosa*) in continuous culture	Population density	60 to 120 h	Nutrient concentration, dilution rate	
Kindig 1979	Algae (*Scenedesmus* sp., *Anabaena* sp., *Chlorella* sp., *Ankistrodesmus* sp., *Selenastrum* sp.) in batch cultures	Population density, optical density	32 to 58 days	Streptomycin	
Klotz et al. 1976	Algae (*Chlorella* sp., *Achnanthes deflexa*) in semicontinuous culture	Population density	7 days	Sewage treatment plant effluent	
Lange 1974	Algae (*Microcystis aeruginosa*, *Nostoc muscorum*, *Phormidium foveolarum*) in batch culture	Population density, pH, COD	31 days		
Marshall 1969	*Daphnia magna*, *D. pulex*	Population density, # gravid females, # males, # shed ephippia, # eggs in brood chambers	100 weeks	Gamma radiation	
Mickelson et al. 1979	Algae (*Thalassiosira gravida*, *Skeletonema costatum*, *Chaetoceros septentrionalis*) in continuous culture	Population density	10 days	Dilution rate	
Mosser et al. 1972	Algae (*Thalassiosira pseudonana*, *Dunaliella tertiolecta*) in batch cultures	Population density, biomass	4 days	PCB, DDT	

Author(s)	System components	Measured responses	Duration of expt.	Expt'l. variables	Validation
Muller and Lee 1977	Ciliate (*Euplotes vannus*), nematode (*Chromadorina germanica*), foramaniferan (*Allogromia laticollaris*)	Population density	42 days	Food density	
Russell and Fielding 1974	See Fielding and Russell 1976	Final yield (biomass)	35 days	Light, temperature, salinity	
Tilman 1977, Titman 1976	Algae (*Asterionella formosa*, *Cyclotella meneghiniana*) in semicontinuous culture	Population density	42 days	Nutrient concentration, dilution rate	
B. *PREDATION*					
Akre and Johnson 1979	Zooplankton (*Anomalagrion hastatum*, *Daphnia magna*, *Simocephalus vetulus*)	Prey survival	12 h	Prey density, prey species, predator hunger	
Baker and Modde 1977	Largemouth bass, bluegill, blacktail shiner	Prey survival	15 min	Stain	
Bethel and Holmes 1977	Amphipods, ducks, muskrats	Prey survival	5 to 15 min (ducks), 24 h (muskrats)	Parasitism	
Brandl and Fernando 1974	Zooplankton (*Acanthocyclops vernalis*, *Ceriodaphnia reticulata*)	Prey survival	5 days	Predator diet, prey size	
Brandl and Fernando 1978	Zooplankton (Cyclops *vernalis*, *Mesocyclops edax*, natural communities)	Prey survival	24 h	Predator density	
Confer 1971	Zooplankton (*Mesocyclops edax*, *Diaptomus floridanus*)	Prey survival	2 to 5 days	Prey size, prey density	
Confer and Blades 1975a,b	Bluegill, *Daphnia magna*, *D. pulex*, natural copepods	Reactive distance, capture success	Seconds	Prey size, light	
Confer et al. 1978	Lake trout, brook trout, *Daphnia magna*, *D. pulex*	Reactive distance	Seconds	Prey size, prey pigmentation, predator hunger, light, aquarium shape	
Cooke 1971	Newt, frog tadpole, gravel	# Attacks, # captures	1 to 5 min	DDT	
Coutant 1973	Rainbow trout, chinook salmon	Prey survival	3 to 10 min	Heat shock	
Coutant et al. 1974	Largemouth bass, channel catfish	Prey survival	30 min	Cold shock	
Deacutis 1978	Killifish, Atlantic silverside, flounder	# Attacks, # captures # escapes	30 min	Heat shock	

Author(s)	System components	Measured responses	Duration of expt.	Expt'l. variables	Validation
Drenner et al. 1978	Gizzard shad, natural zooplankton community	Prey survival	1 to 13½ h		
Eisler 1973	Gastropod drill, mussel	Prey survival, # attacks, predator egg production	28 to 32 days	Crude oil, oil dispersant	
Farr 1977	Killifish, grass shrimp, sand	Prey survival, capture time	3 h	Methyl parathion, ethyl parathion	
Farr 1978	Killifish, grass shrimp, sheepshead minnow, sand	Prey survival	5 days	Methyl parathion	
Goodyear 1972	Largemouth bass, mosquito fish, refuge	Prey survival	20 days	Gamma radiation	
Gerritsen 1978	Zooplankton (*Cyclops scutifer*, *Chaoborus* sp.)	Prey survival	4 h	Prey size	
Herting and Witt 1967	Bowfin, various prey (fish)	Prey survival	24 h	Disease, parasitism handling stress	
Kania and O'Hara 1974	Largemouth bass, mosquito fish, refuge	Prey survival	60 h	Hg	
Kerfoot 1977a, b	Zooplankton (*Cyclops bicuspidatus*, *C. vernalis*, *Bosmina longirostris* -or-	# Encounters, # attacks, # injuries, # ingestions	5 h	Prey instar	
	Epischura nevadensis, *Bosmina longirostris*, *Daphnia ambigua*, *Ceriodaphnia* sp.)	Prey survival	3 days	Prey species, prey size	
Landry 1978	Zooplankton (*Labidocera trispinosa*, *Acartia clausi*, *A. tonsa*, *Paracalanus parvis*, *Calanus pacificus*	Prey survival	24 h	Prey species, prey size, prey density, jar size, anesthesia	
Li and Li 1979	Zooplankton (*Acanthocyclops vernalis*, rotifers, cladocerans, copepods)	Prey survival	24 h	Prey species, prey size	
Luckinbill 1973	Protozoa (*Didinium nasutum*, *Paramecium aurelia*)	Population density	6 to 33 days	Bacterial food, methyl cellulose	
Luckinbill 1974	Protozoa (*Didinium nasutum*, *Paramecium aurelia*)	Population density, population extinction	3 to 80 h	Culture volume	
Mullin 1979	Zooplankton (*Tortanus discaudatus*, *Acartia clausi*)	Prey survival	6 to 8 h	Prey instar, jar size	
O'Brien et al. 1976	Bluegill, *Daphnia magna*	Prey selection	Seconds	Prey size	

Author(s)	System components	Measured responses	Duration of expt.	Expt'l. variables	Validation
Salt 1967	Protozoa (*Woodruffia metabolica*, *Paramecium aurelia*)	Population density, generation time, searching rate, capture rate	~100 h		
Salt 1968	Protozoa (*Amoeba proteus*, *Paramecium aurelia*)	Population density, generation time, feeding rate	~300 h		
Salt 1974	Protozoa (*Didinium nasutum*, *Paramecium aurelia*)	Population density, generation time, feeding rate	6 to 72 h	Prey and predator densities	
Stein 1977	Smallmouth bass, crayfish, gravel	Prey survival, handling time	10 h to 7 days	Prey sex, moulting stage, substrate type	
Stein and Magnuson 1976	Smallmouth bass, crayfish, gravel	Prey behavior	3 days	Presence of predator	
Sullivan et al. 1978	Largemouth bass, fathead minnow, gravel, artifical plants	Prey survival	3 to 7 days	Cd	
Sylvester 1972	Coho salmon, sockeye salmon	Mean survival time	5 to 10 min	Heat shock	
Sylvester 1973	Coho salmon, sockeye salmon	Prey survival	15 min	Heat shock	
Tagatz 1976	Pinfish, grass shrimp, seagrass, sand	Prey survival	1 to 3 days	Mirex	
Thompson 1978	Damselfly nymph, *Daphnia magna*	Attack coefficient, handling time, prey survival	24 h	Prey density, temperature	
Van den Ende 1973	Bacteria (*Klebsiella aerogenes*), protozoa (*Tetrahymena pyriformis*) in continuous culture	Population density	1100 h		
Vaughan 1979	Largemouth bass, bluegill, refuge	Prey survival	Not specified	Viral infection	
Veilleux 1979	Protozoa (*Didinium nasutum*, *Paramecium aurelia*)	Population density, fission rate, feeding rate	Not specified		
Vinyard and O'Brien 1976	Bluegill, *Daphnia magna*	Prey selection	Seconds	Prey size	
Ward et al. 1976	Marsh fiddler crab in salt marsh plots	Population density	6 weeks	Insecticide	
Ware 1972	Rainbow trout, amphipods (*Crangonyx richmondensis*, *Hyalella azteca*), litter substrates	Prey survival, # attacks, # captures, handling time, reactive distance	50 min	Prey density, substrate type, predator hunger	
Werner 1974	Bluegill, green sunfish, *Daphnia magna*	Handling time	Minutes	Prey size, predator hunger	
Werner and Hall 1974	Bluegill, *Daphnia magna*	Prey survival, reactive distance	0.5 to 5 min	Prey size, prey density	

Author(s)	System components	Measured responses	Duration of expt.	Expt'l. variables	Validation
Woltering et al. 1978	Largemouth bass, mosquito fish, refuge	Prey survival predator growth	10 days	NH_3	
Wolters and Coutant 1976	Largemouth bass, bluegill	Prey survival	1 to 30 min	Cold shock	
Yocum and Edsall 1974	Yellow perch, lake whitefish	# Attacks, # captures	30 min	Heat shock	
Zaret 1972	Fish (*Melaniris chagresi*), zooplankton (*Ceriodaphnia* cornutum)	Prey survival	1 h	Prey morphology	
C. PARASITISM					
Couch and Courtney 1977	Shrimp, virus	% Infection, mortality	35 days	PCB	
D. MIXED FLASK CULTURES					
Bryfogle and McDiffett 1979	Flask, water, pond inoculum	P, R, chlorophyll, biomass, populations	48 days	Herbicide	
Cooper 1973	Water, sterile pond sediment, pond water with zooplankton removed	P, R	40 days	Herbivorous fish	
Ferens and Beyers 1972	See Gorden 1967	P, R, chlorophyll, biomass	40 days	Gamma radiation	
Fraleigh 1971	See Gorden 1967	P, R, chlorophyll, biomass, total P	60 days	Phosphorus enrichment	
Gorden 1967	Artificial medium, inoculum from Beyers' original culture (algae, bacteria, *Paramecium*, rotifers, flagellate, ostracod)	P, R, populations, POM, DOM, thiamin, glyoxylate uptake	75 days	None	
Kelly 1971	Artificial medium, inoculum from lakes, ponds, streams	P, R, chlorophyll, carotenoids, biomass, alkalinity, CO_2, DOM, DIM, TOM, TIM, populations	59 weeks	Temperature	
Kurihara 1978a,b (see also Sugiura et al. 1976a,b)	Artificial medium, pond inoculum	P, R, biomass, populations	140 days	B-BHC, Cu	
Leffler 1977	Artificial medium; inoculum from aquaria, Beyers' cultures, ponds	P, R, populations, Element Distribution Index	18 weeks	Temperature	
McConnell 1962	Tap water, pond inoculum	P, R, organic matter	222 days	Nutrients	
McConnell 1965	Tap water, pond inoculum; *Tilapia* added later	P, R, fish biomass	1½ months	Herbivorous fish	
Neill 1972, 1975	Well water, algae, crustacea	P, populations, crustacean gut contents, microhabitat, survivorship, fecundity	>1 year	*Gambusia* predation	

Author(s)	System components	Measured responses	Duration of expt.	Expt'l. variables	Validation
Ollason 1977	Artificial medium, inoculum from horse trough	Populations	60 days	Light levels	
Reed 1976	Water, pond inoculum, various substrates.	Populations	20 weeks	Nutrient enrichment	
Thomas 1978	Water, inoculum from various sources	Pigments, POM		Cd, nitrogen	
Waide et al. 1978	Artificial medium, pond inoculum	DO, pH, temp., conductivity, turbidity, fluorescence, total P, SRP, algal populations	70 days	Turbulence, light regime, pH, Daphnia grazing	
Taub (1969a,b,c; 1976; Taub and Crow 1980; Taub, Crow, and Hartman 1980; Crow and Taub 1979)	Bacteria, algae, Daphnia, protozoa, rotifers, ostracod, artificial medium, sediment	Population density, pigments, optical density, biomass, productivity	1 to 2 months	Algicide, insecticides, organic enrichment, Hg, Cd, PCB	
E. PERIPHYTON COMMUNITIES					
Admiraal 1977	Recirculating sea water, natural periphyton on natural sediment	Chlorophyll, populations	4 to 23 weeks	Source of sediment, nutrient enrichment	
Bott et al. 1977	Recirculating stream water, periphyton colonizers, various substrates	Carbon flux; litter decomposition; NTA decomposition		Cu	Compared w/natural stream
Cushing and Rose 1970	Recirculating river water, periphyton colonizers, glass tube substrate	^{65}Zn uptake		None	
Gerhart et al. 1977	Partially recirculating lake water, model stream, periphyton colonizers, porcelain substrates	Chlorophyll, populations, biomass	25 days	Coal leachate	
Kedhe and Wilhem 1972	Recirculating stream water, periphyton colonizers, snails, microscope slide substrates	Biomass, chlorophyll, populations	92 days	Grazing	
Kevern and Ball 1965	Recirculating artificial medium, periphyton inoculum on rock substrates	Water chemistry, P, R	>1 month	Temp., light, EDTA	
McIntire et al. 1964	Partially recirculating stream water in wooden troughs, gravel, periphyton colonizers	P, R, biomass, chlorophyll, populations	2 years	None	
McIntire 1968a,b	As above, plus snails	"		Light, temp.	
Phinney and McIntire 1965	"	"		Temp.	

Author(s)	System components	Measured responses	Duration of expt.	Expt'l. variables	Validation
F. OTHER MODEL ECOSYSTEMS					
Medine et al. 1980; Porcella et al. 1976	Homogenized sediment, artificial medium, air, and sediment biota	Nutrient dynamics, ecosystem metabolism	80 to 120 days	Heavy metals	
Pritchard et al. 1979	Intact sediment core, natural water, sediment biota	(Biodegradation and contaminant transport)	8 to 21 days	Organic contaminants	
Dudzik et al. 1979; Harte et al. 1978, 1980; Jassby et al. 1977a,b	Artificial medium, natural lake plankton	Population dynamics, nutrient concentrations	6 weeks to several months	Phenol, NH_4, Fe	
Harris et al. 1980	Natural sediment, pond water, macrophyte community, and associated biota	Ecosystem metabolism, nutrient dynamics, water chemistry, taxonomic groups	2 to 12 months	Arsenic, coal-derived oil	
Brockway et al. 1979	Sand, natural sediment, river water, detritus	Ecosystem metabolism, nutrients, water chemistry	Undetermined		
Eggert et al. 1979	Natural sediment, pond water, pond biota	(Biodegradation and contaminant transport)	2 to 4 months	Organic contaminants	

APPENDIX B*

SUMMARY TABLE OF TERRESTRIAL TEST SYSTEMS

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*Complete references can be found in Section 4.3.

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APPENDIX B
SUMMARY TABLE OF TERRESTRIAL TEST SYSTEMS[a]

Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
4.1 Population interactions						
4.1.1 Competition						
(1) Microbes Rennie and Schmidt 1977	Natural populations of two Nitrobacter species in NO_2-enriched soils in screwcap tubes.	Number of bacteria, oxidation rate.	14 (exp)[b]	Moderate		
(2) Plants Bennett and Runeckles 1977	Seeds of grass and clover are seeded as monocultures and a mixture in 15.6-cm pots of a fertilized soil mix and thinned to 12 plants per pot.	Leaf area, weight of parts, number of tillers.	42 (exp)	Low	Ozone	In progress
(3) Arthropods						
(a) Drosophila Ayala 1969	Adult flies added to 0.47-L bottles with culture medium (simplest and most common system).	Number of adults, adult weight, ratios of weight and numbers by sex, wing length, viability, length of life stages, and time to extinction.	18 to 23 (generation)	Low	Radiation	
(b) Other flies						
Housefly-blowfly Pimentel et al. 1965	Houseflies and blowflies in 9.5x13.3x19-cm boxes with vials of larval medium, either singly or in sets of 4 or 16 boxes connected by plastic tubing.	Numbers of adults and time to extinction.	>14 (generation)	Moderate (1 cell), high (16 cell)		
Blowfly-blowfly Ullyett 1950	Newly hatched larvae of 2 blowfly species are placed on 140 g of beef in a 45x45x10-cm box.	Larva and puparium weight and length, fecundity, sex ratio, mortality, number at each life stage.		Moderate		
(c) Tribolium Park 1957	Adult beetles added to 8 g of flour and yeast in a shell vial in an incubator.	Number of adults and larvae and time to extinction.	180-1000 (extinction) 30 (generation)	Moderate		

Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
(d) Other grain insects Crombie 1945	Adult insects or eggs are added to 10 g of cracked wheat in jars in an incubator.	Number of adults, fecundity, longevity, length, and weight.	∼ 365 (exp)	Low		
(e) Soil arthropods Longstaff 1976	Collembola are maintained in a 15.7-cm^2 x 3-cm dish with a floor of moist plaster of Paris, charcoal, and yeast.	Number of individuals by size class.	84 to >168 (exp)	Low		
Anderson 1978	Microarthropods are removed by drying from intact 9x9x10-cm litter-soil columns in plastic containers and replaced with the competing species.	Number of individuals by soil horizon and microhabitat.	14 (exp)	Moderate		Numbers and distribution were compared to the field.
4.1.2 Herbivory						
(1) Sucking insects						
(a) Aphid-alfalfa	No system developed.					
(b) Aphid-grain Windle and Franz 1979	2 Cultivars of barley planted together and singly, 69 seeds/25.5-cm pot with 100 aphids/pot contained by cellulose nitrate collars.	Number of barley leaves and tillers, height, and dry weight. Number of aphids and damage.	14 to 42 (exp)	Moderate		
(c) Whitefly-plant	See 4.1.3(2)(b)					
(d) Scale-plant	No system developed.					
(2) Chewing insects Grasshopper-grass Dyer and Bokhari 1976	Blue gramma grass grown in a flask of nutrient solution with a grasshopper contained on the plant top by a screen cage.	Changes in solution pH, plant growth; grasshopper intake rate, digestive efficiency, growth, and amount of litter cut.	18 (exp)	Moderate		
Corn-rootworm-corn Ortman and Branson 1976	Newly hatched rootworms are added to plastic pouches of soil containing corn seedlings.	Growth rate and % survival of rootworms.	10 (exp)	Low		

Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
4.1.3 Predation						
(1) Microbes Habte and Alexander 1975	10^{10} *Xanthomonas* cells were added to 10 g of sterile and non-sterile soil in 150 mL dilution bottles.	Counts of bacteria and predators.	3 (exp)	Moderate		
(2) Arthropods						
(a) Parasitoid-gall midge Force 1970	40 *Baccharis* seedlings in small pots are placed in groups of 10 at weekly intervals into 48x38x40-cm screen cages. Eight adult midges are added with each group of plants, and 1 to 4 species of wasps are added at appropriate times.	Life table statistics for the wasps; frequency of parasitism and multiparasitism.	60 to 200 (exp)	High		
(b) Parasitoid-whitefly Mechols and Tauber 1977	Tobacco plants were held in 1-m^3 screen cages. Individual adult whiteflies were allowed to oviposite within single-leaf cages, and newly emerged parasitoids were added at different intervals for 8 to 12 h.	Parasitization rate; parasitoid and whitefly development and mortality.		Moderate		
McClanahan 1970	Eight potted cucumbers in an isolated 3.2x5.2-m section of greenhouse were exposed to 690 adult whiteflies, and 15 days later, 210 adult parasitoids. Pesticide was sprayed at intervals.	Numbers of parasitized and unparasitized whiteflies over time and numbers of adult whiteflies and parasitoids at termination.	75 (exp)	Moderate	Oxthioquinox	

Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
(c) Parasitoid-aphid Force and Messenger 1964, 1965	Aphids were raised on alfalfa stems in vials of water within 3.5x15-cm glass tubes held vertically in an environmental chamber. Host and parasitoid densities and number of parasitoid species were varied.	Parasitoid survival, development rate, fecundity, and percent parasitization and super parasitization of the host.	1 (hunting) 9 to 38 (development)	Moderate		
(d) Predator-aphid Murdock and Marks 1973	Single ladybird larvae were placed on potted bean plants with different ratios of two aphid species. Plants were isolated by "Fluon"-coated plastic collars.	Prey selection, predator, and prey behavior.	0.36 (hunting)	Moderate		
(e) Parasitoid-grain moth Benson 1974	Moths and wasps were raised in 90x90x75-cm cages with 81 cardboard trays containing 50 g of wheat-feed each. Nine trays were replaced each week.	Numbers of wasps and moths by developmental stage.	35 (moth life cycle) 59 (exp)	Moderate		
(f) Parasitoid-bean weevil Utida 1957	Bean weevils were raised on beans in petri dishes and exposed to one or two species of parasitoids.	Number of weevils and wasps.	21 (weevil life cycle) 1050 (exp)	Moderate		
(g) Parasitoid-fly Pimentel et al. 1963	Single 9.5x13.3x19-cm plastic boxes or arrays of 16 or 30 boxes connected by 0.64-cm plastic tubes containing vials of fly medium, parasitoid wasps, and houseflies or blowflies.	Numbers of flies and wasps	42 to 132 (extinction of single cell system) 133 to 224 (16 cell system) 574 (30 cell system)	Moderate		

Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
(h) Ground-dwelling beetles Harris and Oliver 1979	Staphylinid beetles preyed on horn fly eggs and larvae on manure pats placed on a soil-vermiculite mixture on a 32x28x5-cm piece of sod covered with mesh.	Number of emerging flies.	14 (fly development)	Moderate		
(i) Spiders Hardman and Turnbill 1974	7.5-cm^3 boxes or arrays of eight 7.6x7.6x 5.6-cm trays with "Fluon"-coated sides connected by 25x24-cm arched plastic bridges. Predators and prey were subadult lycosid spiders and vestigial-winged Drosophila.	Number of flies killed.	6 (hunting)	Moderate		
(j) Mites Huffaker 1956	Two groups of 36 field-infected potted strawberries were arranged on greenhouse benches. One group was sprayed with parathione to eliminate the predator.	Numbers of predators and prey.	<9 to 365 (predator effect seen, length of experiment)	Moderate		
Huffaker et al. 1963	Mite herbivores and predators were placed on a random subset of 252 partially covered oranges, which rested in glass coasters on 3 wire mesh shelves, which were connected by wooden dowels.	Numbers of predators and prey.	450 (maximum length of experiment)	Moderate		
4.1.4 Parasitism	No systems discussed.					
4.1.5 Symbiosis						
(1) Lichens	No systems discussed.					
(2) Rhizobium-Legume Pareek and Gaur 1970	Inoculated seeds sown in pots of seived soil that had been sprayed with pesticide.	Plant and seed weight and N content, number of nodules, and leghaemoglobin content.	28 to 91 (nodule formation-plant maturation)	Moderate	>40 pesticides and ozone	Some field studies have been done, but not to validate laboratory studies.

Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
(3) Mycorrhizae Wilde and Persidsky 1956	Seedlings in pots of soil inoculated with mycorrhizal fungi in a greenhouse.	Plant weight, number of fungal propagules, % of root length infected.	240 (exp)	Moderate	Numerous pesticides	
4.2 Ecosystems						
4.2.5 Synthetic systems						
(1) Soil Atlas et al. 1978	Sieved soil in a flask, bottle, or other container.	Microbe numbers, respiration, nutrient dynamics, enzyme assays, ATP assays.	1 to >100 (exp)	Low	Many chemicals	Informal; decades of experience indicate general validity.
(2) Litter Spalding 1979	Sorted litter in a container.	Respiration and enzyme assays.	1 to 28 (time to response)	Low	7 heavy metals	None; related generally to field studies.
(3) Litter and soil Bond et. al. 1976	Sieved soil (150 g) and seived litter (15 g) in a beaker or lined can in a gas and temperature control system.	Respiration, heat output, microbe numbers.	20 (exp)	High	20 metal salts, O_3, and SO_2	None; related generally to field studies.
(4) Gnotobiotic soil Coleman et. al. 1977	*Pseudomonas* sp. *Acanthamoeba* sp., and *Mesoplogaster* sp. in 20 g of dried, sifted, and sterilized soil in a 50-mL Erlenmeyer flask.	CO_2 efflux, N and P mineralization and immobilization and numbers of bacteria, protozoa, and nematodes.	14 (exp)	High		
(5) Plant and soil (a) Pot Eno and Everett 1958	7.6-L pots of field soil with 10 bean plants.	Plant germination, plant production, microbe numbers, respiration, and nitrification.	17 (exp)	Moderate	10 insecticides	
(b) Lichtenstein et al. 1977	Layers of toxicant-contaminated and uncontaminated homogenized soil with corn plants, in a 86-mm-diameter, 1-L plastic cylinder mounted on a leachate collecter.	Toxicant fate, (soil, plant, and leachate); plant biomass; plant symptoms.	22 (exp)	Low	Phorate, Stauffer N-2596, Eptam, and Phorate	Compared to field trial for N-2596.

Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
(c) Agroecosystem chamber Nash et al. 1977	Crop plants grown on 15 cm of seived soil in a 115-cm-high x 150 cm x 50 cm closed glass box.	Toxicant fate (air, soil, leachate and plant).	35 (exp)	Moderate	Toxaphene, DDT, Silvex, Zineb, Maneb	
(6) Soil, litter, plant and animal						
(a) Odum Odum and Lugo 1970	Natural soil, litter, a flowering plant, fern, moss, lichen, and algae in a 16.2-cm-diameter plastic desiccator.	CO_2 exchange.		Moderate	Radiation	Compared to the radiated forest from which the components were derived.
(b) Witkamp Witkamp and Frank 1970	Round containers 7 to 13-cm-diameter by 10 to 13-cm with a leachate port, soil or sand, litter, millipedes, snails, and seedlings.	Mineral nutrient dynamics, CO_2 efflux, and litter weight.	98 (exp)	Moderate		
(c) Metcalf Metcalf et al. 1979	Corn seedlings grown in vermiculite or soil with earthworms, isopods, slugs, saltmarsh caterpillars, and a vole in a 19-L wide-mouth jar. Ports in the lid and base permit air and leachate sampling.	Pesticide fate, plant growth, and faunal numbers.	20 (exp)	Moderate	15 pesticides	Pesticide fate is comparable to that reported from the field.
(d) Terrestrial microcosm chamber Gile and Gillett 1979	A 1x0.75x0.6-m glass box with 20 cm of synthetic soil, alfalfa, ryegrass, nematodes, earthworms, enchytraeid worms, isopods, mealworms, crickets, snails, and a pregnant vole. Ports allow air and leachate sampling.	Pesticide fate, faunal numbers, and vole behavior.	67 (exp)	High	Dieldrin	Compared to published field and laboratory studies of dieldrin.

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Test system	Components	Measured responses	Response time (days)	Cost	Perturbations tested	Validation
4.2.6 Excised systems						
(1) Soil core Jackson et al. 1977	5-cm-diameter x 5- or 10-cm intact soil core encased in heat-shrunk plastic and supported on a leachate collecter.	Nutrient loss, respiration, toxicant loss, and degradation. Microbe biomass, soil enzymes.	30 to 59 (exp)	Low	As, dieldrin, methyl parathion, 2, 4, 5-T, and hexachlorobenzene.	None.
(2) Grassland core Jackson and Levine 1978; Van Voris et al. 1978	15 to 30-cm-diameter x 10 to 25-cm grassland cores encased in plastic and supported on a leachate collecter.	Toxicant loss and uptake, nutrient loss, soil ATP, CO_2 flux, plant biomass, soil arthropod, nematode, bacteria, and fungi.	100 to 175	Moderate	As, Cd	
(3) Sod Campbell 1973	16-cm diameter x 7-cm-deep sod in a nalgene jar.	Respiration, photosynthesis, plant symptoms, species abundance.	<1 (time to response of respiration and photosynthesis) 45 (plant damage symptoms)	Moderate	Radiation	None
(4) Treecosm Jackson et al. 1978	An intact block of forest soil 45x45x25-cm with one ~2-m sapling and associated ground flora sealed with epoxy in wood boxes.	Transport, nutrient loss, respiration, ATP, microbe density, primary production.	300 (exp)		Pb smelter dust	Yes; results are qualitatively but not quantitatively confirmed by field studies and modeling.
(5) Outcrop McCormick and Platt 1962	Excised 90x90-cm segments of granite outcrop communities arranged in a 1x6.5-m concrete trough.	Plant growth; plant reproduction, plant species density, soil erosion.	365 (exp)	High	Radiation	In terms of natural properties, but not response to toxicants.

[a] The study cited is representative of the system type described. Measured responses and perturbations are listed for all known experiments of each type, not just the study cited.

[b] Notes in parentheses indicate how response time was determined; (exp) indicates that the length of the experiment, which may be arbitrary, was used.

APPENDIX C

ALPHABETICAL BIBLIOGRAPHY
AQUATIC AND TERRESTRIAL TEST SYSTEMS

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APPENDIX D

SECTIONAL BIBLIOGRAPHY

AQUATIC AND TERRESTRIAL TEST SYSTEMS

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3. AQUATIC TEST SYSTEMS

3.1.3 COMPETITION

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4.2.6 EXCISED SYSTEMS

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